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CONTENTS

Studies in Antibiosis between Bacteria and Fungi—III. Inhibitory Action of Some Actinomycetes on Various Species of Fungi in Culture ..... *Const. J. Alexopoulos and J. Arthur Herrick* 237

A Pollen Study of Lake Sediments in the Lower Willamette Valley of Western Oregon ..... *Henry P. Hansen* 265

Vegetational Studies in Areas of Sedimentation in the Bonnet Carré Floodway ..... *Julian A. Steward and Wm. T. Penfound* 281

The Genus Cephalocarpus Nees (Cyperaceae) ..... *Charles L. Gilly* 290

North American Ranunculi—IV ..... *Lyman Benson* 299

Mass Collections: Dierville lonicera ..... *Norman C. Fassett* 317

Index to American Botanical Literature 323

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BULLETIN OF THE TORREY BOTANICAL CLUB
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STUDIES IN ANTIBIOSIS BETWEEN BACTERIA AND FUNGI—III. INHIBITORY ACTION OF SOME ACTINOMYCETES ON VARIOUS SPECIES OF FUNGI IN CULTURE[1]

CONST. J. ALEXOPOULOS AND J. ARTHUR HERRICK

In a previous article (1) it was reported that of 80 *Actinomyces* species grown with *Colletotrichum gloeosporioides* on agar, 14 proved to be strong inhibitors, 31 weak inhibitors, and 35 had no visible effect upon the growth of that fungus and consequently were classified as non-inhibitors.

In order to determine whether inhibition is a function of the *Actinomyces* alone or of both the *Actinomyces* and the fungus, two species of *Actinomyces* from each of the above categories were selected and grown with each of nine species of fungi representing various fungous groups.

MATERIALS AND METHODS

The same technique used in previous experiments (1), was adopted again, of inoculating the *Actinomyces* in two places on the agar, 4 cm. apart, and five days later inoculating the fungus midway between the resulting *Actinomyces* colonies. As before, the criterion of inhibition was either a flattening of the fungous colonies on the sides nearest the *Actinomyces* colonies, or a distinct general stunting of the fungous colony as compared with the growth of the control plates in which the fungus was grown alone (1, 2).

The organisms used in these studies were as follows:

Actinomycetes:

1. Strong inhibitors of *C. gloeosporioides* (1).
   Actinomyces annulatus Beij.
   Actinomyces madurae (Vinc.) Lehm. et Neum.
2. Weak inhibitors of *C. gloeosporioides* (1).
   Actinomyces flavovirens Waks.
   Actinomyces gougeroti Duché
3. Non-inhibitors of *C. gloeosporioides* (1).
   Actinomyces hasltedii Waks. et Curt.
   Actinomyces viridochromogenus Kr.

Fungi:

Phycomyces blakesleeanus Burg.
Acanthorhynchus vaccinii Shear
Sclerotinia sclerotiorum (Lib.) Massee
Glomerella cingulata (Stonem.) Sp. et v. Schr.
Phoma betae Frank

[1] A preliminary report of this investigation was presented at the Cleveland meeting of the Ohio Academy of Science, May 9, 1941.

The writers are indebted to Dr. H. A. Cunningham, Head Department of Biology, Kent State University, for his encouragement and cooperation in providing research facilities.

[THE BULLETIN for March (69: 167–256) was issued March 2, 1942]

Botrytis cinerea Pers.
Alternaria solani (Ell. et Mart.) J. et Gr.
Stereum gausapatum Fries, Strain S–12 (3)
Fomes fraxinophilus (Pk.) Sacc.

The medium used was prepared according to the following formula:

Glucose	30 gms.
Peptone	5 gms.
K_2HPO_4	1 gm.
Agar	20 gms.
Water	1000 cc.

The pH of the agar was adjusted to 8.1 and after sterilization at 15 lbs. for 15 minutes it was found to be 6.8. Fifteen cubic centimeters of agar were

TABLE 1. *Growth of nine species of fungi on glucose agar, grown in association with six species of Actinomyces, expressed in terms of average diameters, in millimeters, of at least four cultures*

Fungi	Age of fungous colonies in days	Actinomycetes						
		Control	*A. halstedii*	*A. viridochromogenus*	*A. flavovirens*	*A. gougeroti*	*A. annulatus*	*A. madurae*
Phycomyces blakesleeanus	3	73 × 76	64 × 68	68 × 72	62 × 70	5 × 11	46 × 62	41 × 66
	5	90 × 90[a]	.....	.....	.....	8 × 39	.....	.....
	10	.....	.....	.....	.....	8 × 90	.....	.....
Acanthorhynchus vaccinii	3	11 × 13	15 × 16	15 × 16	16 × 16	5 × 5	17 × 18	15 × 17
	5	16 × 20	25 × 30	30 × 31	28 × 30	10 × 13	26 × 32	23 × 32
	10	32 × 32	.....	.....	.....	16 × 35	.....	.....
Sclerotinia sclerotiorum	3	25 × 27	35 × 45	45 × 40	45 × 45	11 × 30	25 × 39	17 × 45
	5	90 × 90	.....	.....	.....	20 × 90	34 × 90	.....
	10	.....	.....	.....	.....	26 × 90	.....	.....
Glomerella cingulata	3	38 × 38	32 × 40	32 × 36	34 × 36	14 × 21	29 × 35	19 × 38
	5	72 × 73	.....	.....	.....	17 × 40	38 × 68	29 × 73
	10	.....	.....	.....	.....	24 × 83	.....	.....
Phoma betae	3	30 × 30	31 × 32	29 × 29	28 × 29	9 × 12	27 × 31	20 × 30
	5	59 × 59	.....	34 × 58	34 × 58	11 × 20	35 × 58	29 × 58
	10	.....	.....	.....	36 × 90	15 × 50	.....	.....
Botrytis cinerea	3	28 × 27	27 × 30	29 × 29	29 × 33	7 × 8	24 × 29	16 × 29
	5	70 × 70	.....	.....	33 × 76	17 × 24	33 × 75	24 × 73
	10	.....	.....	.....	.....	28 × 90	.....	36 × 90
Alternaria solani	3	33 × 32	31 × 32	32 × 35	31 × 32	8 × 16	25 × 32	23 × 33
	5	57 × 58	.....	.....	36 × 58	16 × 30	36 × 58	30 × 58
	10	.....	.....	.....	.....	20 × 72	.....	.....
Stereum gausapatum	3	14 × 15	15 × 16	21 × 20	18 × 18	8 × 10	16 × 16	14 × 14
	5	33 × 33	27 × 30	43 × 49	30 × 43	13 × 19	35 × 35	31 × 38
	10	70 × 70	.....	.....	38 × 90	21 × 57	.....	.....
Fomes fraxinophilus	3	9 × 9	10 × 10	10 × 10	10 × 10	trace	10 × 10	10 × 10
	5	18 × 18	16 × 19	21 × 21	18 × 18	7 × 8	20 × 20	17 × 20
	10	42 × 42	35 × 40	.....	33 × 37	16 × 16	37 × 44	30 × 42

[a] 90 × 90 denotes that the whole surface of the agar is covered with fungous growth.

poured into each Petri dish. Six plates were inoculated for each test as well as six controls for each fungus. Each figure presented is based on the average of at least four plates. Two measurements of the diameter of each fungous colony were taken at intervals of 24 hours beginning 2 days after the inoculation of the fungus and continuing for 8 days, or until the fungous and *Actinomyces* colonies were in contact.

RESULTS

The measurements obtained as outlined above are summarized in table 1. The first figure represents the average diameter of the fungous colony in the direction of the *Actinomyces* colonies. This figure itself, in table 1, sometimes exceeds 40 mm., which is the distance between the *Actinomyces* colonies, because the fungous sometimes grows over the *Actinomyces* or completely surrounds it, in the interval between 24-hour measurements. This may happen even after temporary inhibition of fungous growth by a weak inhibitor has taken place. The second figure represents the average diameter of the fungous colony at right angles to the first. At the first signs of inhibition, the distance between the fungus and *Actinomyces* was measured on both sides and the average recorded as "inhibitory distance" (2). Inhibitory distances between various combinations of fungi and actinomycetes are summarized in table 2.

TABLE 2. *Average inhibitory distances between 6 species of Actinomyces and 9 species of fungi, expressed in millimeters*

Fungi	*A. halstedii*	*A. viridochromogenus*	*A. annulatus*	*A. madurae*	*A. flavovirens*	*A. gougeroti*
Phycomyces blakesleeanus	0	0	6	5	3	15
Acanthorhynchus vaccinii	7	0	8	9	6	15
Sclerotinia sclerotiorum	1	0	7	12	1	15
Glomerella cingulata	1	3	9	11	1	13
Phoma betae	1–	1	5	12	2	14
Botrytis cinerea	5	0	7	13	3	16
Alternaria solani	0	1	5	11	1–	13
Stereum gausapatum	5	1–	0	3	3	13
Fomes frazinophilus	9	2	3	10	3	15

DISCUSSION

Employing the same standards as in previous experiments (1), i.e., classifying actinomycetes as "strong inhibitors" if the inhibitory distance at which they become effective is 10 or more millimeters, and as "weak in-

hibitors'' if the inhibitory distance is less than 10 mm., we may now reclassify the six species used in these experiments with respect to their effect upon the growth of the nine fungi against which they were tested.

The four actinomycetes selected from those which inhibited *C. gloeosporioides* in previous experiments (1), also inhibit the nine fungi employed here with the exception that *A. annulatus* fails to inhibit *S. gausapatum*.

A. halstedii and *A. viridochromogenus*, which had been classified as non-inhibitors of *C. gloeosporioides* (1), may or may not inhibit other fungi, but when they do inhibit, they do so weakly, as shown by their inhibitory distances. An exception is found with *A. halstedii* against *F. fraxinophilus*, between which the inhibitory distance is rather great; this is shown in table 2.

There was considerable discrepancy in the behavior of strong and weak inhibitors against various fungi. *A. annulatus*, which was selected as a strong inhibitor, proved to be a weak inhibitor in all tests but one in which it failed to inhibit the growth of the fungus. On the other hand, *A. madurae*, also selected as a strong inhibitor, proved to be a strong inhibitor in six tests and a weak inhibitor in three (table 2). *A. flavovirens* and *A. gougeroti* were selected as weak inhibitors on the basis of their effect on *C. gloeosporioides* (1). *A flavovirens* was a weak inhibitor of all other fungi as well, but *A. gougeroti* proved to be a very strong inhibitor of all other fungi employed in these experiments (table 2).

In evaluating the results discussed above, it must be borne in mind that no natural dividing line exists between so-called strong and weak inhibitors, and that the inhibitory distance of 10 mm. which is used as a dividing line between the two categories has been selected arbitrarily. As shown in table 2 the inhibitory distances vary from less than 1 to 16 mm.

It will be noted from the figures presented in table 1, that, in some cases, the fungi, notably *Acanthorhynchus vaccinii* seem to grow better in the presence of some actinomycetes than in the control plates; in spite of that, inhibitory distances between colonies of these organisms are recorded in table 2. A further examination of the figures in such cases will show that the diameter of the fungous colony between the Actinomyces colonies (first figure) is considerably smaller than the diameter at right angles (second figure), showing that as the margin of the fungous colony approached the *Actinomyces* its rate of growth was retarded as compared to the rate of growth at right angles. Furthermore, such fungous colonies were generally distinctly flattened on the sides nearest the *Actinomyces* colonies leaving no doubt as to the inhibitory action taking place. Photographs of this effect have been published in a previous article (2).

On the other hand, the fact that in some cases the fungus grows better,

in at least one direction, in the presence of the *Actinomyces* than in the controls, may very well be an indication of the presence of growth stimulating substances secreted in the agar in addition to, or instead of, the inhibitory substances. That such growth stimulating substances are manufactured by various microorganisms is well established. This phase of the problem is being investigated.

SUMMARY AND CONCLUSIONS

1. Actinomycetes differ in their ability to inhibit the growth of a given fungus in culture under the conditions of the experiment.

2. Fungi differ in their susceptibility to inhibition by a given species of *Actinomyces*.

3. The degree of inhibition of fungous growth is a function of both the fungus and the inhibiting organism.

4. No correlation seems to exist between the normal rate of growth of a fungus and the degree of its inhibition by a given *Actinomyces*.

5. No correlation seems to exist between the relative position of a fungus in the accepted system of classification and the degree of its inhibition by a given *Actinomyces*.

6. There is some evidence that some of the species of *Actinomyces* employed in these experiments, may be manufacturing a growth promoting substance in addition to, or instead of growth inhibiting substances.

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A POLLEN STUDY OF LAKE SEDIMENTS IN THE LOWER WILLAMETTE VALLEY OF WESTERN OREGON[1]

HENRY P. HANSEN

The occurrence of peat deposits beyond the limits of Pleistocene glaciation in the Pacific Northwest is uncommon. Sphagnum bogs are rare except along the Pacific Ocean where the moist, equable climate is favorable for their development. In the Willamette Valley of western Oregon, the small amount of precipitation during the growing season is probably the chief reason for the absence of sphagnum bogs. The author has made a pollen study of the only extensive one known to exist in this area (Hansen 1941a). Sedge, tule, reed, and cat-tail swamps or bogs are also uncommon, but they may be occasionally found on floodplains, in abandoned stream channels, and in oxbow lakes. Many of these areas have been drained for agricultural purposes, and often practically all evidence of their previous existence has been obliterated. Floodplain associes of willow, cottonwood, alder, ash, and largeleaf maple also mark the presence of hydroseres that are rapidly nearing the climax stage of plant succession. Many of these areas are merely alluvial floodplains where the water table remains sufficiently high during the summer to permit the growth of moisture-loving species. Few of these areas, however, have an accumulation of peat or other pollen-bearing sediments suitable for the purpose of pollen analysis. It is fortunate, therefore, that several peat deposits satisfactory for pollen analysis are present in the lower Willamette Valley. Their pollen record serves as a valuable accession to the problem of post-Pleistocene forest succession and climate in the Pacific Northwest. The Willamette Valley is a rather distinct floristic province within an otherwise more or less homogeneous hemlock-cedar forest climax of this region.

ORIGIN AND CHRONOLOGY OF THE SEDIMENTS

The peat profiles for this study were obtained from two different deposits. Two profiles were obtained from the Labish Flats, located about 4 miles northeast of Salem, Oregon. Lake Labish was formerly a shallow lake before it was drained in 1912 for agricultural purposes. The lacustrine sediments cover an area about 9 miles long and one-half mile wide. The elevation is between 140 and 150 feet above sea level. The upper end of the former lake is separated from the Willamette River by a divide not over two miles wide and about 30 feet high. The width and depth of the channel and the adjacent

[1] Published with the approval of the Monographs Publication Committee, Oregon State College, as Research Paper No. 53 of the School of Science, Department of Botany.

topography indicate that it is an abandoned course of the Willamette River. The channel was probably occupied by a distributary of a braided stream. The lake was evidently ponded by a delta deposited by the Pudding River. Later the Willamette River receded and the present channel carried its water. The Pudding River follows the old Willamette Channel from the lower end of Lake Labish, emptying into the present Willamette River farther north and downstream. The level of Lake Labish was maintained by smaller streams debouching into it. One of them is now the Little Pudding River.[2] Peat samples of the profiles were taken at quarter-meter intervals with a Hiller peat borer. One profile was taken in section 31 of T. 6 S., R. 2 W., and the other was obtained in section 21 of the same township. The depth of the lacustrine sediments in both profiles is 7 meters. The depth has been somewhat reduced since drainage, by consolidation, oxidation, and deflation. The surface of the sediments has been lowered by at least 3 feet, and undoubtedly some of the original surface has been lost through deflation. Shorelines of the original lake exist from 15 to 25 feet above the present surface. The lowest level sampled consists of fine sand and silt which grades into clay at 6.5 meters. The clay changes to gray-brown sedimentary peat at 5 meters, which in turn grades into brown fibrous peat at 4 meters. The last type continues to the surface and becomes coarser upward in the profiles. Both profiles are essentially the same with respect to the thickness of the various types of sediments. *Hypnum* moss leaves are present throughout the fibrous peat. A layer of pumice less than an inch thick occurs at 1.75 meters in both profiles. It is not possible to state the source of the pumice because there have been several active volcanoes in the Cascades of Oregon during the post-Pleistocene (Williams 1935, 1941). A bog about 13 miles west of Bend, Oregon, has two layers of pumice, while bogs farther south in the Cascade Range rest on a thick mantle of pumice. The latter evidently came from the eruption of Mount Mazama, which resulted in the formation of the caldera holding Crater Lake.

A third profile of lacustrine sediments was sampled at Onion Flat, about 2 miles northeast of Sherwood, Oregon. This deposit lies about 30 miles north of Lake Labish, and 10 miles south of Portland, at an elevation between 130 and 140 feet above sea level. The peat and other pollen-bearing sediments have accumulated in a former channel of the Tualatin River which rises in the Coast Range to the west and empties into the Willamette River about 2 miles south of Oregon City.[3] Samples were obtained in section 21 of T. 2 S., R. 1 W. The depth of the sediments in the area of sampling is 12 meters. This bog has also been drained and the present surface is not that which existed before drainage. The bog is underlain with sand and gravel which grade into

[2] U. S. Geol. Surv. Topogr. map, Mount Angel Quadrangle, Oregon.
[3] U. S. Geol. Surv. Topogr. map, Oregon City and Tualatin Quadrangles, Oregon.

silt at 12 meters. Fine clay with considerable organic matter present occurs from 12 to 9 meters. The stratum between 9 and 5 meters consists of a gray-brown sedimentary peat, and fibrous peat is present from 5 meters to the surface. The surface sediments seem to have been more oxidized than those at Labish Flats. No definite stratum of pumice or ash is discernible with the naked eye, but volcanic glass is abundant at 0.5 and 0.75 meters. This suggests that a greater thickness of surface sediments has been removed than at Labish Flats, where the pumice layer occurs at 1.75 meters. It is probable that the pumice and glass had the same origin. In none of the profiles, therefore, is the forest succession recorded by tree pollen to the present time. Each year the surface is plowed, so that the upper several inches of peat are not suitable for pollen analysis. The uppermost sample of each profile was obtained from the highest undisturbed horizon.

Peat deposits formed in depressions lying on glaciated sites may be readily dated with their maximum ages. The Willamette Valley, however, was not glaciated during the Pleistocene. The mountain glaciers in the Cascade Range a few miles to the east apparently were of insufficient magnitude to reach the Willamette Valley, nor was the Coast Range to the west glaciated (Fenneman 1931). During the melting of the last stage of the Wisconsin glacier, the Willamette Valley was inundated by backwater from the glacier-swollen Columbia River (Bretz 1919). The water reached a height of several hundred feet above the valley floor as is evidenced by the occurrence of ice-rafted erratics (Allison 1935). This inundation suggests that any peat deposits or other types of lacustrine sediments on the Willamette Valley floor are of postglacial origin. As previously stated, Lake Labish was ponded in an abandoned channel of the Willamette River, probably a distributary of the main stream when it carried a greater volume of water than at present. The Onion Flat sediments were deposited in a former channel of the Tualatin River, although it apparently was not an oxbow left by a meandering stream. It was probably formed when the Tualatin River carried a greater volume of water than the main channel could hold, and spilled over as a distributary to further erode small tributary valleys. These channels must have been occupied by their respective streams when there was considerably more water available from their hydrographic basins than at present. This probably occurred during the early post-Pleistocene when there was heavy precipitation as well as an abundance of meltwater from wasting mountain glaciers. It is hard to say how long these channels were occupied by their respective streams. If they were abandoned soon after the recession of the continental ice sheet to the north and subsidence of glacial water in the Willamette Valley, the sediments of this study had their initiation in early post-Pleistocene. The 12-meter depth of the Onion Flat profile and the forest succession recorded in the lower half suggests that this is probably true.

Twelve meters of sediments, largely organic, are of considerable magnitude, especially in the Willamette Valley where the summers are dry and far from the optimum for the maximum rate of peat deposition. The average depth of 16 post-Pleistocene peat deposits west of the Cascades in Oregon, Washington, and British Columbia is about 31 feet, as shown by profiles in a study by Rigg and Richardson (1938). Most of these deposits lie in regions climatically favorable to rapid peat accumulation. It is realized that climate is not the only factor that controls the rate of organic sedimentation, but peat deposits in the dryer regions east of the Cascades, in Washington, average about 19 feet in depth (Hansen 1941g). The depth of the Onion Flat sediments is almost twice that of Labish Flats. The rate of peat deposition may vary in the same region, but the relative thickness and proportions of clay, sedimentary, and fibrous peat indicate that the former represents a longer period of time, and not merely a more rapid rate of sedimentation. The thickness of sedimentary peat is about 4 meters, whereas that of Lake Labish is only 1 meter. Sedimentary peat probably has the slowest rate of deposition of the several types of sediments present, and such a great difference in its thickness in the two profiles suggest a much earlier origin for the Onion Flat sediments. The thickness of fibrous peat is also much greater in the latter profile. The writer believes that the sediments of Onion Flat were initiated much earlier than those of Lake Labish, and that they date from extremely early post-Pleistocene.

In preparation of the sediments for microscopic examination, the potassium hydrate method was used. One hundred or more pollen grains of indicator species were identified from each level. The number of pollen grains of nonsignificant species was also recorded and listed in the tables. Few or no pollen grains are present in the levels of the bottom meter of the Labish profile. These horizons are not included in the tables or pollen profile diagrams. The identification of the winged conifer pollen was based upon the size range of the pollen of the several species within each genus. This method has been described by the author in several previous papers (Hansen 1941a, 1941b, 1941d). No attempt was made to separate the pollen of Sitka spruce (*Picea sitchensis*) from that of Engelmann spruce (*P. Engelmanni*). It probably consists chiefly of the former, which is abundant along the coast a few miles to the west, while Engelmann spruce is largely confined to the upper slopes of the east side of the Cascade Range. Those species recorded by their pollen as 1.5 per cent or less are listed in the tables as 1 per cent.

FORESTS IN ADJACENT AREAS

The Willamette Valley is from 25 to 30 miles wide and about 125 miles long. It lies within the Humid Transition life zone (Bailey 1936). It is also included in the hemlock-cedar climax of the Coast Forest (Weaver and

Clements 1938), but because of the low summer rainfall the forests are few and scattered. Little or no western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*) are present. The valley is intensively cultivated and most of the virgin forests have been removed, but the coniferous forests were never as dense as those of either the Coast and Cascade Ranges (Peck 1941). The principal coniferous species is Douglas fir (*Pseudotsuga taxifolia*) which grows on slopes and better drained areas. Oregon white oak (*Quercus garryana*) is the chief broadleaf tree, and usually occurs in groves. It is difficult to say what the successional relationship is between these two species, because they are often found growing together. The chief other coniferous species present is lowland white fir (*Abies grandis*) which thrives in low areas along the streams or other moist habitats. Farther south scattered specimens of western yellow pine (*Pinus ponderosa*) occur, while in certain localized areas groves of this species exist. On the floodplains of streams and other moist sites grow associes of cottonwood (*Populus trichocarpa*), willow (*Salix lasiandra*), Oregon ash (*Fraxinus oregana*), red alder (*Alnus rubra*), largeleaf maple (*Acer macrophyllum*), and vine maple (*A. circinatum*). It can be seen that the forests of the Willamette Valley are abundant neither in extent nor in the number of species.

The eastern slope of the Coast Range is forested largely with Douglas fir with an occasional hemlock. The summers are apparently too dry for the latter species to thrive. Pollen analysis of a sphagnum bog in the east foothills of the Coast Range and farther to the south shows that hemlock has not been nearly so abundant as Douglas fir during that part of the postglacial period represented by the peat deposit (Hansen 1941a). On the west slope of the Coast Range the precipitation increases and western hemlock becomes more abundant at the expense of Douglas fir. Along the coast is a strip composed largely of Sitka spruce and western hemlock, and along the immediate ocean on the stabilized sand dunes and other sandy soil thrives lodgepole or shore pine (*Pinus contorta*). Pollen analyses of two bogs on the Oregon Coast show that western hemlock and Sitka spruce have been predominant during the post-Pleistocene (Hansen 1941d). On a few of the higher peaks of the Coast Range noble fir (*Abies nobilis*) occurs, while western white pine (*Pinus monticola*) and silver fir (*A. amabilis*) have been recorded at several stations in the northern part. On the western slope of the Cascade Range facing the northern part of the Willamette Valley, the forests are composed chiefly of Douglas fir, with western hemlock increasing in abundance with the altitude. Also at higher elevations thrive western white pine, silver and noble fir, lodgepole pine, western red cedar, and Englemann spruce. The last is not so common on the west as the east slope. Near timberline, mountain hemlock (*Tsuga Mertensiana*), alpine fir (*Abies lasiocarpa*), white-bark pine (*P. albicaulis*), and Alaska cedar (*Chamaecyparis nootkatensis*) flourish.

The presence of pollen in the sediments from all or most of these species justifies the mention of their occurrence in adjacent areas. Less significant species, as far as pollen analysis is concerned, that thrive on favorable sites in the Willamette Valley and adjacent slopes of the Coast and Cascade Mountain Range are *Arbutus menziesii, Castanopsis chrysophylla, Corylus californica, Myrica californica, Cornus occidentalis, Osmaronia cerasiformis, Philadelphus gordonianus, Amelanchier florida, Prunus emarginata, Ceanothus sanguineus, Crataegus douglasii, Symphoricapos albus,* and *Ribes sanguineum.*

Forest Type Maps (1936) designate the Willamette Valley as non-forested and agricultural lands, and the adjacent mountain slopes as Douglas fir types of various size classes. It is also included in the Pacific Douglas fir forest under the classification by Shantz and Zon (1924). Over most of the hemlock-cedar climax west of the Cascades, Douglas fir is a subclimax species that has been able to persist as one of the chief dominants because of periodic fires (Munger 1940). In western Oregon, however, western hemlock is almost absent and Douglas fir is not likely to be replaced by the former even if no periodic fires occur. The climate is too dry. It would be hard to say what the climax vegetation is for the Willamette Valley, but it appears that the climate and edaphic conditions are such as to form a tension area in which Douglas fir and white oak are in equilibrium at present. An increase in summer rainfall probably would permit an increase in Douglas fir as subclimax to western hemlock, while a decrease in the annual precipitation would perhaps cause a trend toward an oak-grassland sere.

The Willamette Valley is designated as having a humid microthermal climate, with a summer deficiency of precipitation (Thornthwaite 1931). The average mean annual rainfall for five stations in the valley, within a radius of 25 miles to both bogs, is 43.5 inches. About 10 per cent of this occurs during May to August, inclusive (Weather Bur., U.S.D.A., 1936). The elevation of these stations ranges from 400 to 57 feet above sea level. At Glenora, in the northern part of the Coast Range, and less than 50 miles from Onion Flat, the mean annual precipitation is 130 inches. At Government Camp on Mt. Hood, at an elevation of 3800 feet and about 60 miles from either peat deposit, the annual mean precipitation is about 85 inches. Thus the Willamette Valley is bordered by areas with very moist climate, which has undoubtedly influenced the pollen record of the forest trees in the peat profiles. The general direction of the wind during the period of anthesis is westerly, which suggests that the forests of the Coast Range are more strongly represented than those of the Cascades. This is also somewhat corroborated in the pollen profiles themselves.

FOREST SUCCESSION

There is no reason to assume that the Willamette Valley, the Coast Range,

and unglaciated parts of the Cascades were not forested during the Pleistocene when areas to the north were covered with ice. Forests grow to the edge of mountain glaciers at present, and even upon certain glaciers in Alaska (Washburn 1935). The climate of the Pleistocene during continental glaciation, however, may have been more severe, but it was probably sufficiently mild in western Oregon to support forests. The forests that existed within range of pollen dispersal to the site of Onion Flat during the time represented by the lower 6 meters of sediments were composed almost entirely of lodgepole pine, Sitka spruce, and lowland white fir (fig. 1). Lodgepole pine

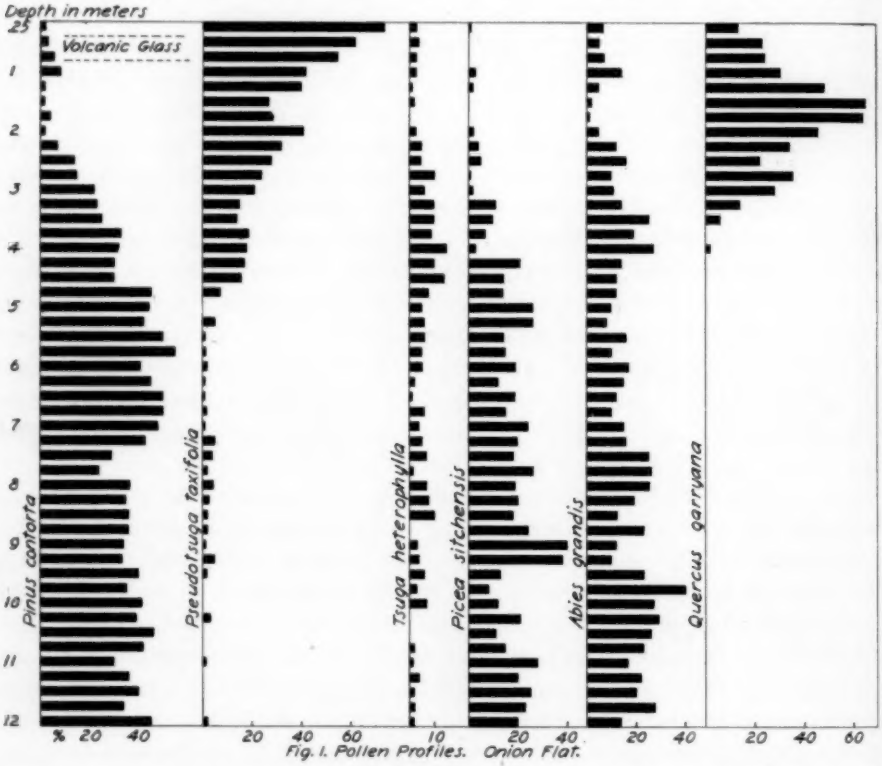

Fig. 1. Pollen Profiles. Onion Flat.

proportions fluctuate from 24 to 50 per cent with an average of about 40 per cent. Sitka spruce fluctuates from 8 to 40 per cent and lowland fir varies from 10 to 40 per cent. While the pollen percentages of lodgepole pine run higher than those of spruce and fir, it does not necessarily mean that it was predominant, since lodgepole sheds a greater quantity of pollen than Sitka spruce, and probably more than lowland white fir. It is interesting to note that lodgepole pine and Sitka spruce are entirely absent from the Willamette Valley and the east slope of the Coast Range at present. These two species may be over-represented by their pollen because of its transportation by

water. The Tualatin River rises in the Coast Range so that its drainage area is in proximity to the spruce and lodgepole forests of the Pacific Coast. During high water in the spring the Tualatin River may have spilled over into its former channel occupied by the accumulating Onion Flat sediments. Pollen from the coast forests reached the streams and were carried into the lake and incorporated with the sediments. The relatively low proportions of western hemlock pollen in these horizons, however, do not substantiate this theory, or perhaps hemlock was not as abundant during early post-Pleistocene as it is today on the coast. It was apparently predominant during most of the post-Pleistocene on the Oregon Coast (Hansen 1941d).

Lodgepole pine continues its predominance upward in the Onion Flat profile to the 3.75 meter level. It is also recorded by its pollen as the principal species with fir and spruce in the lower 2.5 meters of the Lake Labish profiles (figs. 2, 3). As previously stated, the greater depth of the Onion Flat profile

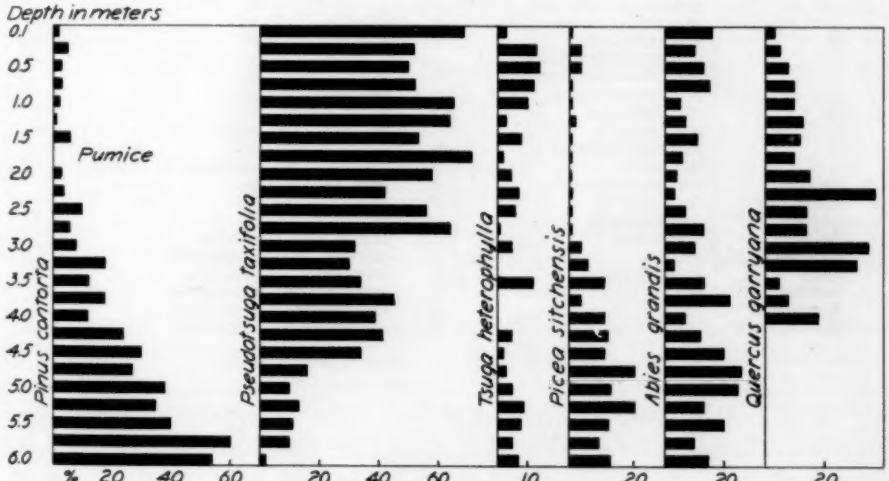

Fig. 2. Pollen Profiles. Lake Labish. No. 1.

indicates a longer period of time for its sedimentation than that of Lake Labish. It seems possible that the upper 7 meters of the former are contemporaneous with the entire Lake Labish profiles. They also are 7 meters deep, but, as stated above, the lower meter is practically devoid of pollen. The pollen spectra of the principal species recorded correlate remarkably well in the upper 6 meters of all three profiles, which substantiates the theory of their synchronism. The predominance of lodgepole pine for such a long period of time as portrayed in the Onion Flat profile is significant. In several other bogs analyzed for their fossil pollen that lie beyond the glaciated region, lodgepole pine is not recorded as the predominant species in adjacent areas (Hansen 1939c, 1941a, 1941c, 1941d, 1941f). This suggests that the

adjacent forests had reached a climax when the lowest pollen-bearing sediments were deposited or had remained more or less stabilized during the glacial period, or at least during the latter part. The forests apparently had not been destroyed during glaciation nor had conditions favorable for an invasion by lodgepole developed. This was true even along the Oregon Coast where lodgepole pine thrives at present (Hansen 1941d). In a bog farther south in the Willamette Valley, in the east foothills of the Coast Range, Douglas fir is recorded as having been predominant during the entire period represented by the profile (Hansen 1941a). Either the sediments do not record all of the postglacial, or lodgepole was not abundant in this region

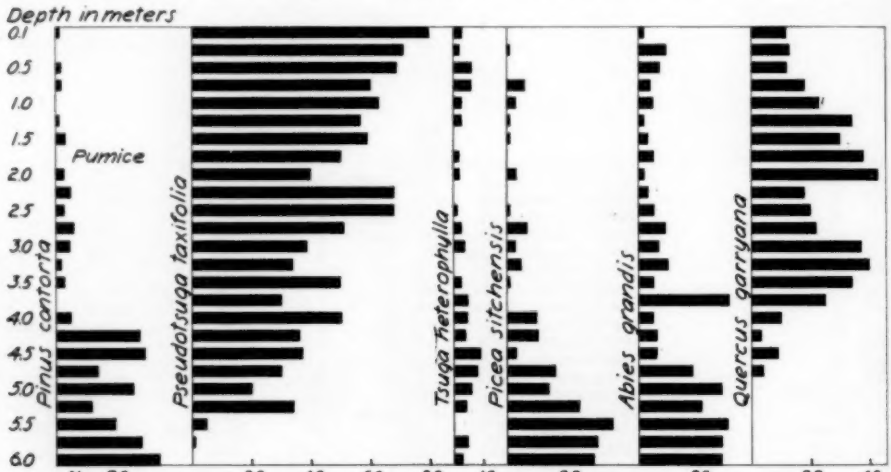

Fig. 3. Pollen Profiles. Lake Labish. No. 2.

at any time during the post-Pleistocene. In other peat deposits that lie within the glaciated region, lodgepole pine was the predominant species recorded in the bottom sediments. As these sediments are usually sand and silt, it seems probable that pioneer postglacial forest succession was recorded. It is believed that lodgepole pine flourished near the ice-front because of lack of competition of other species for which the climatic and edaphic conditions were unfavorable. As the environment became moderated and somewhat stabilized, other species invaded and replaced lodgepole because of its greater intolerance for shade and shorter life span. This was evidently true both east and west of the Cascade Range in Washington (Hansen 1938, 1939a, 1939b, 1940a, 1940b, 1941b, 1941e). The comparative absence of Douglas fir and western hemlock in the lower horizons of all profiles suggests that the edaphic and climatic conditions were unfavorable for these species. The high proportions of Sitka spruce and lowland white fir, both moisture-loving species, suggests that the climate was very wet. Heavy precipitation and melting of

the glaciers in the Cascades may have resulted in erosion in the hills and inundation in the valley, with constantly changing edaphic and topographic conditions. Lodgepole pine was able to survive in abundance because of its ability to live under an adverse climate and unstable edaphic conditions, and its early seed-bearing age. The latter characteristic permits it to migrate more readily and re-establish itself under changing edaphic and topographic conditions than the other species. This is evidenced by its invasion of pumice-covered areas in the Cascades of southern Oregon, burns, sphagnum bogs, and sand dunes along the Pacific Coast. The pollen percentages of lodgepole pine generally decline upward in all profiles from their maxima in the lower levels and become negligible in the upper horizons (figs. 1, 2, 3). Sitka spruce and lowland white fir are most abundantly recorded in the lower levels of the Labish profiles as well as in the other. In one of the former they both show higher proportions at several levels than lodgepole pine (fig. 3). Spruce is the first to show a decline and it is recorded by negligible percentages in the upper 3 meters of all profiles. Lowland white fir maintains higher proportions in the higher horizons, indicating that conditions remained more favorable nearer to the present time for this species than for spruce. Lowland white fir is common in the Willamette Valley today, and is recorded to 16 per cent in the top level of one of the Labish profiles (fig. 2).

Douglas fir is recorded by its pollen in low proportions in the lower 7 meters of the Onion Flat profile with a maximum of 5 per cent at 3 levels (fig. 1). It likewise is represented by slight percentages in the lower horizons of the Lake Labish profiles (figs. 2, 3). This is consistent with its trend in the Puget Sound region (Hansen 1938, 1940a, 1941b). It increases sharply from 4.75 meters in the Onion Flat profile and from 5 and 5.5 meters in the others, to attain 74, 69, and 80 per cent respectively in the uppermost level. In its general increment upward toward the top, Douglas fir shows a number of fluctuations of considerable magnitude. The greatest of these variations occurs conversely with those in the pollen spectra of Oregon white oak and will be discussed later. Bogs located within the hemlock-cedar climax of the Coast Forest in the Puget Lowland of western Washington show Douglas fir as rapidly replacing the pioneer forests of lodgepole and western white pine (Hansen 1938, 1940a, 1941b). It was in turn replaced more gradually by western hemlock to some extent, but was able to persist in equal abundance with the latter, owing to periodic fires that interrupted forest succession toward the hemlock-cedar climax. It did not, however, attain so high proportions as in the profiles of this study. In eastern Washington, Douglas fir has played a minor part in postglacial succession because of the dry climate (Hansen 1939b, 1940b, 1941f). On the Pacific Coast of Oregon and on the west side of the Olympic Peninsula it also has been unimportant in the forest complex during the post-Pleistocene (Hansen 1941c, 1941d). Douglas fir has

been predominant on the east slope of the Coast Range in west central Oregon during most of the postglacial period (Hansen 1941a).

The pollen of white oak does not make its appearance in the lower levels of the profiles. In the Onion Flat profile it is first recorded at 4 meters by 1 per cent, and in the others at 4.57 and 4.75 meters with 10 and 4 per cent respectively (figs. 1, 2, 3). The fact that this species is not recorded by its pollen in the lower levels in the Onion Flat profile is further evidence that this profile represents a much longer period of time. Oak soon increases sharply after its initial appearance, being recorded as 35 per cent at 2.75 meters in the Onion Flat profile, and 35 and 40 per cent at 3 and 3.25 meters respectively in the Lake Labish sediments. In the latter, Douglas fir shows abrupt declines at these same levels. Oak then precipitately declines to 22 per cent in the Onion Flat profile at 2.5 meters, and to 14 and 18 per cent at 2.5 and 2.25 meters respectively in the other two. It again increases to 65 per cent in the former at 1.5 meters, and to 37 and 43 per cent at 2.25 and 2 meters respectively in the Lake Labish sediments. These are the highest proportions attained in the white oak spectra. That these maxima are all approximately synchronous is denoted by the occurrence of the pumice layer immediately above in the Labish profiles and slightly higher in the other (figs. 1, 2, 3). The general trend of Douglas fir increment is again interrupted at the oak maxima, showing a decline to less than the oak proportions in the Onion Flat and one of the Labish profiles. It should be noted that this increase and decrease of oak and Douglas fir respectively are not merely relative. There is an actual decrease in the frequency of Douglas fir pollen at these horizons. White oak declines from these maxima, and is recorded by 13, 3, and 12 per cent in the uppermost horizons. In a bog near Tacoma, Washington, located on the Tacoma "prairies," oak is recorded by its pollen to as high as 14 per cent in the middle horizons of a 10.5 meter peat profile (Hansen 1938). This area is characterized by scattered groves of white oak on the gravelly soil of the outwash plain from the Vashon glacier of the Puget Sound region. The oak maximum in this bog may be synchronous with those of this study. It seems possible that white oak is under-represented, because of the vast areas on either side of the Willamette Valley forested with Douglas fir, while oak is and probably always has been confined to the valley. Also from the writer's observations it seems probable that oak does not produce as much pollen as Douglas fir.

Western white pine is recorded by its pollen to higher proportions in the lower levels of all profiles and declines to only a trace near the top (tables). This trend is consistent with that of most peat profiles west of the Cascade Range. Western hemlock is the most abundantly recorded of the other conifers. In the Onion Flat profile it attains its greatest abundance in the middle horizons, as it does in one of the others. In the third, it shows its

TABLE 1

Percentages of Fossil Pollen. Onion Flat Profile

Depth in meters	*Pinus contorta*	*P. monticola*	*P. ponderosa*	*Pseudotsuga taxifolia*	*Tsuga heterophylla*	*T. mertensiana*	*Picea sitchensis*	*Abies grandis*	*A. nobilis*	*A. lasiocarpa*	*Thuja plicata*	*Quercus garryana*	*Pinus* spp.*	*Abies* spp.*	*Alnus**	*Salix**	Cyperaceae*	*Typha**	*Nymphozanthus**
0.25	2	.....	...	74	3	...	1	7	.....	.....	.....	13	.....	.....	5	156	4	3	.....
0.5	3	1	2	62	4	...	.....	5	.....	.....	.....	23	1	1	3	198	.....	.....	.....
0.75	5	2	4	55	3	...	.....	7	.....	.....	.....	24	1	1	4	94	.....	.....	.....
1.0	8	1	...	42	3	...	3	15	.....	.....	.....	30	.....	.....	2	208	.....	.....	.....
1.25	2	2	...	40	1	...	2	5	.....	.....	.....	48	2	.....	.....	35	.....	.....	.....
1.5	2	1	...	27	2	...	.....	2	.....	.....	1	65	1	.....	5	27	7	1	.....
1.75	4	2	...	29	.....	...	.....	1	.....	.....	.....	64	1	.....	.....	15	.....	1	.....
2.0	2	1	1	41	3	...	2	5	.....	.....	.....	45	1	.....	2	12	3	.....	.....
2.25	7	5	...	32	5	...	4	12	.....	.....	1	34	3	.....	1	10	.....	1	.....
2.5	14	3	7	28	5	...	5	16	.....	.....	.....	22	3	.....	1	3	.....	.....	.....
2.75	15	4	...	24	10	1	1	10	.....	.....	.....	35	.....	.....	3	10	.....	.....	.....
3.0	22	2	...	21	6	...	2	11	.....	.....	8	28	3	1	1	4	6	.....	.....
3.25	23	11	...	15	10	2	11	14	.....	.....	.....	14	2	.....	.....	4	1	.....	1
3.5	25	...	4	14	13	...	10	25	3	.....	.....	6	7	.....	.....	2	2	1	1
3.75	33	2	8	19	9	1	7	19	.....	.....	2	.....	4	.....	4	2	3	23	26
4.0	32	2	2	18	15	...	3	27	.....	.....	.....	1	3	3	3	4	5	60	32
4.25	30	2	...	17	10	...	21	14	.....	2	4	.....	9	3	12	5	.....	3	4
4.5	30	10	...	16	14	4	14	12	.....	.....	.....	.....	4	2	1	2	.....	3	.....
4.75	45	8	2	7	8	1	14	12	1	2	.....	.....	8	1	.....	9	3	2	.....
5.0	44	7	...	...	5	3	26	10	2	3	.....	.....	3	.....	1	12	3	3	2
5.25	42	10	...	5	6	3	26	8	.....	.....	.....	.....	7	3	1	.....	5	4	.....
5.5	50	5	1	1	6	2	14	16	1	4	.....	.....	9	.....	.....	1	8	4	.....
5.75	55	10	1	1	5	...	15	10	.....	3	.....	.....	11	1	.....	6	.....	2	.....
6.0	41	10	...	2	5	4	19	17	.....	2	.....	.....	14	3	.....	4	1	2	.....
6.25	45	20	2	1	2	1	12	15	1	1	.....	.....	15	1	.....	5	1	5	.....
6.5	50	7	3	1	1	4	19	12	1	2	.....	.....	7	2	.....	3	.....	7	.....
6.75	50	10	2	2	6	5	15	10	.....	.....	.....	.....	12	2	3	1	5	4	.....
7.0	48	3	...	1	4	3	24	15	1	1	.....	.....	7	1	.....	5	7	8	.....
7.25	43	.....	1	5	5	5	20	16	3	2	.....	.....	9	4	.....	9	11	5	.....
7.5	29	5	4	4	7	8	18	25	.....	.....	.....	.....	11	3	.....	3	.....	4	.....
7.75	24	8	4	2	1	7	26	26	1	1	.....	.....	5	2	.....	2	8	.....	.....
8.0	36	6	2	4	7	2	19	25	.....	.....	.....	.....	6	3	.....	.....	2	.....	.....
8.25	35	13	...	3	8	1	20	19	1	.....	.....	.....	7	1	.....	1	2	.....	.....
8.5	36	12	2	2	10	6	18	12	.....	2	.....	.....	2	1	.....	7	5	1	.....
8.75	36	6	2	2	...	2	24	23	.....	5	.....	.....	6	1	.....	4	.....	.....	.....
9.0	34	6	...	1	3	4	40	12	.....	.....	.....	.....	17	5	.....	3	1	1	3
9.25	33	4	...	5	4	4	38	10	1	1	.....	.....	12	2	.....	1	2	1	.....
9.5	40	10	2	2	6	4	13	23	.....	.....	.....	.....	6	3	.....	7	2	4	.....
9.75	35	8	...	.....	3	2	8	40	4	.....	.....	.....	7	1	.....	2	.....	.....	.....
10.0	41	13	...	.....	7	...	12	27	.....	.....	.....	.....	9	6	.....	1	1	.....	.....
10.25	39	6	...	3	.....	2	21	29	.....	.....	.....	.....	14	2	.....	5	.....	.....	.....
10.5	46	11	2	.....	.....	3	11	26	1	.....	.....	.....	1	4	1	.....	1	1	.....
10.75	42	12	4	.....	2	1	15	23	1	.....	.....	.....	11	3	.....	4	2	.....	.....
11.0	30	16	5	1	1	1	28	17	1	.....	.....	.....	7	1	.....	2	.....	.....	.....
11.25	36	8	6	.....	4	4	20	22	.....	.....	.....	.....	5	2	.....	1	.....	.....	.....
11.5	40	10	...	.....	2	2	25	20	.....	1	.....	.....	7	2	1	.....	5	.....	.....
11.75	34	13	...	.....	2	...	23	28	.....	.....	.....	.....	5	1	2	.....	4	.....	.....
12.0	45	14	...	2	2	2	20	14	1	.....	.....	.....	12	3	.....	.....	1	2	.....

* Number of pollen grains; not computed in the percentages.

highest frequencies in the lower two-thirds. Its maximum is 15 per cent in any of the profiles (tables). The climate has probably been too dry for this species in the Willamette Valley. In the Puget Lowland it partially replaced Douglas fir, to become equally abundant during the latter half of the post-glacial. Mountain hemlock is appreciably recorded in the lower two-thirds of the Onion Flat profile, and to only a trace in a few levels of the others (tables 1, 2, 3). Neither western nor mountain hemlock shows a trend that correlates with the spectra of the other species. Pollen of the latter probably drifted down from higher altitudes in the Cascades, or less probably from the northern part of the Coast Range. Western yellow pine is recorded sporadically in the lower horizons and more consistently in the higher levels. This trend differs from that in the bog farther south in the Willamette Valley, where it is more abundantly recorded in the lower levels (Hansen

TABLE 2

Percentages of Fossil Pollen. Labish Profile No. 1

Depth in meters	*Pinus contorta*	*P. monticola*	*P. ponderosa*	*Pseudotsuga taxifolia*	*Tsuga heterophylla*	*T. mertensiana*	*Picea sitchensis*	*Abies grandis*	*A. nobilis*	*Thuja plicata*	*Quercus garryana*	*Pinus* spp.*	*Abies* spp.*	*Alnus**	*Salix**	Cyperaceae*	*Typha**	*Nymphozanthus**
0.10	2	.....	5	69	3	.....	1	16	1	.....	3	1	3	3	.....	1	.....	.....
0.25	5	.....	9	52	13	.....	4	10	1	1	5	2	2	2	15	.....	.....	.....
0.5	3	.....	8	50	14	.....	4	13	.....	.....	8	.....	1	6	43	6	1	.....
0.75	3	.....	7	52	12	.....	1	15	.....	.....	10	3	3	1	32	6	.....	.....
1.0	2	.....	7	65	10	.....	1	5	.....	.....	10	.....	.....	1	15	1	1	1
1.25	1	2	8	64	3	.....	2	7	.....	.....	13	1	2	8	117	3	.....	.....
1.5	6	.....	8	53	8	1	1	11	.....	.....	12	.....	.....	1	12	.....	2	2
1.75	1	.....	9	71	2	.....	1	6	.....	.....	10	2	1	5	.....	7	1	.....
2.0	3	1	13	58	5	.....	1	4	.....	.....	15	.....	.....	.....	10	1	6	1
2.25	4	.....	5	42	7	.....	1	3	.....	1	37	1	1	1	3	1	3	1
2.5	10	.....	6	56	6	.....	1	7	.....	.....	14	2	.....	.....	15	2	2	.....
2.75	6	1	.....	64	1	.....	1	13	.....	.....	14	1	2	3	10	3	7	.....
3.0	8	4	.....	32	5	.....	4	10	2	.....	35	1	1	7	3	9	3	2
3.25	18	.....	12	30	.....	.....	6	3	.....	.....	31	5	1	.....	8	1	.....	1
3.5	12	8	2	34	12	.....	12	13	2	.....	5	3	1	1	39	7	.....	.....
3.75	18	.....	.....	46	.....	.....	4	22	2	.....	8	2	3	6	23	3	.....	2
4.0	12	.....	12	39	.....	.....	12	7	.....	.....	18	4	2	.....	25	5	1	1
4.25	24	5	.....	41	5	.....	13	12	.....	.....	.....	6	1	5	19	2	.....	3
4.5	30	2	.....	34	2	.....	12	20	.....	.....	.....	7	7	.....	21	.....	.....	.....
4.75	27	3	.....	16	3	.....	22	26	3	.....	.....	3	6	1	15	1	.....	2
5.0	38	1	.....	10	7	.....	14	25	3	2	.....	5	5	.....	12	3	.....	.....
5.25	35	7	.....	13	9	.....	22	13	1	.....	.....	7	4	4	7	3	.....	.....
5.5	40	4	.....	11	8	.....	13	20	2	2	.....	12	3	.....	5	.....	.....	1
5.75	60	5	.....	10	5	.....	10	10	.....	.....	.....	15	1	2	3	1	.....	.....
6.0	54	6	.....	2	7	.....	14	15	1	.....	.....	17	3	3	.....	.....	.....	.....

* Number of pollen grains, not computed in the percentages.

1941a). Its trend in this study is more logical, however, because it is the most xerophytic of the conifers, and should have increased during later postglacial time, if a drier climate prevailed. Other species recorded by their pollen are willow, sedge, yellow pond lily, cat-tail, alder, hazel, ash, and maple (tables 1, 2, 3). The first four record the progress of hydrarch succession. The scarcity of alder pollen is unusual because it is generally abundant in most peat profiles in the Pacific Northwest. In some cases alder seems to be correlated with Douglas fir, which suggests that it invades low, damp areas that have been denuded by fire (Hansen 1941a).

CLIMATIC CONSIDERATIONS

In this study the pollen spectra of Sitka spruce, lowland white fir, Douglas fir, and white oak are the best indicators of climatic trends. Spruce is an

TABLE 3

Percentages of Fossil Pollen. Labish Profile No. 2

Depth in meters	*Pinus contorta*	*P. monticola*	*P. ponderosa*	*Pseudotsuga taxifolia*	*Tsuga heterophylla*	*T. mertensiana*	*Picea sitchensis*	*Abies grandis*	*A. nobilis*	*Quercus garryana*	*Pinus* spp.*	*Abies* spp.*	*Alnus**	*Salix**	Cyperaceae*	*Typha**	*Nymphozanthus**
0.10	1	.....	2	80	3	.....	.....	2	.....	12	1	.....	2	3	.....	3	.....
0.25	.....	.....	4	71	2	.....	1	9	.....	13	.....	2	3	1	.....	4	.....
0.50	2	.....	4	69	6	.....	.....	7	.....	12	2	1	.....	2	.....	.....	.....
0.75	2	.....	4	60	6	.....	6	4	.....	18	1	.....	1	1	.....	.....	.....
1.0	.....	.....	3	63	3	.....	3	5	.....	23	.....	1	.....	9	.....	.....	2
1.25	1	.....	2	57	3	.....	1	2	.....	34	.....	.....	7	7	.....	2	1
1.5	3	.....	4	59	.....	.....	1	3	.....	30	1	.....	4	12	.....	.....	.....
1.75	.....	.....	5	50	2	.....	.....	5	.....	38	.....	.....	2	15	2	.....	1
2.0	3	.....	6	40	2	.....	3	2	1	43	2	1	.....	21	5	.....	15
2.25	5	.....	5	68	.....	.....	.....	3	1	18	1	.....	1	14	4	5	1
2.5	3	.....	2	68	1	.....	1	5	.....	20	.....	.....	.....	18	.....	2	5
2.75	6	1	1	51	3	.....	7	9	.....	22	3	1	1	32	.....	1	1
3.0	5	2	3	39	4	.....	3	7	.....	37	.....	.....	1	27	8	7	3
3.25	2	5	.....	34	1	.....	5	10	3	40	1	1	.....	48	9	3	2
3.5	3	.....	2	50	3	.....	1	5	2	34	1	3	3	53	1	4	1
3.75	.....	.....	10	30	5	.....	.....	30	.....	25	2	.....	2	17	4	1	.....
4.0	5	4	1	50	5	.....	10	5	10	10	1	2	7	9	2	1	.....
4.25	28	13	.....	36	4	.....	10	6	.....	3	5	.....	.....	12	7	.....	.....
4.5	30	6	.....	37	9	.....	3	6	.....	9	8	1	5	42	4	1	.....
4.75	14	8	.....	30	8	.....	16	18	2	4	9	2	.....	112	.....	2	.....
5.0	26	6	.....	20	6	.....	14	28	.....	.....	11	3	1	59	5	.....	.....
5.25	12	.....	.....	34	4	2	24	20	4	.....	5	1	.....	216	3	.....	.....
5.5	20	10	.....	5	.....	.....	35	30	.....	.....	7	3	2	.....	1	.....	1
5.75	29	7	.....	1	5	.....	30	28	.....	.....	9	3	3	.....	.....	.....	.....
6.0	35	5	.....	.....	3	.....	29	28	.....	.....	5	2	.....	.....	.....	.....	.....

* Number of pollen grains, not computed in the percentages.

indicator of extremely moist conditions, whereas white oak thrives under the driest climate. Lowland white fir is next to spruce in its moisture requirements, and Douglas fir will survive under drier conditions than either spruce or lowland white fir, but not so xeric as oak. Lodgepole pine is a poor climatic indicator because of its wide climatic and geographic range. The predominance of its pollen in the lower levels of the Pacific Northwest peat profiles marks its invasion of primary areas before the edaphic and physiographic conditions had been stabilized and sufficiently moderated to permit the entrance of other species more tolerant of shade and with a longer life span to replace it. Western hemlock thrives under a moist climate, but it is too sparsely represented in the peat profiles of this study to serve as a climatic indicator. Its low pollen frequency, however, in itself denotes that too dry conditions prevailed for its existence in the Willamette Valley, at least during the latter two-thirds of the post-Pleistocene. Western white pine is indicative of a cool and subhumid climate, and mountain hemlock marks at least a cool climate. Yellow pine is almost as xerophytic as white oak.

In the Puget Lowland of western Washington, postglacial forest succession has probably been more a result of competition than due to climatic change. This also seems to have been true of the Oregon Coast and the west side of the Olympic Peninsula (Hansen 1941c, 1941d). In drier regions where the annual precipitation or summer rainfall is at a critical minimum, slight changes may influence forest succession over a period of time. The greater response of tree growth in dry areas is shown by comparative studies of radial increment in trees living in wet and dry climates (Douglass 1936). In dry climates, slight variations in the annual precipitation are readily reflected by the width of the annual rings, whereas in moister climates the ring width may vary only slightly from year to year, in spite of appreciable differences in the annual rainfall. It is believed that the small amount of summer rainfall in the Willamette Valley is responsible for recording more definite postglacial climatic trends than elsewhere west of the Cascade Range. High percentages of Sitka spruce and lowland white fir pollen in the lower half of the Onion Flat profile mark a wet climate during the first third of the post-Pleistocene. A continuation of proportions of appreciable but lesser magnitude upward in this profile, as well as in the contemporaneous horizons of the lower Lake Labish profiles, marks a persistence of the wet climate for some time longer. The scarcity or absence of spruce pollen in the upper horizons of all profiles and the absence of this species east of the Coast Range at present, substantiates this interpretation. The predominance of lodgepole pine as denoted in the lower strata marks the presence of unstable soil and physiographic conditions, possibly caused by increased surface water from melting glaciers in the Cascades and greater precipitation in the valley. This probably resulted in considerable erosion, deposition,

inundation, emergence, and other changing environmental conditions under which trees requiring 25 years or more to reach seed-bearing age could not persist. The invasion and rapid increase in Douglas fir signify a drier climate and more stabilized edaphic and physiographic conditions as the postglacial period progressed. Instead of the entrance and development of western hemlock to attain equal abundance with Douglas fir, as occurred in the Puget Lowland, white oak invaded the valley and rapidly increased in its extent to supersede Douglas fir at some levels in its pollen proportions. This significant increase at the expense of Douglas fir marks further desiccation of the climate. The maximum of this trend was apparently reached just prior to the eruption of one of the Cascade volcanoes and the deposition of pumice in the accumulating sediments. This period of maximum dryness, as portrayed by the influx of oak, is not corroborated by a simultaneous invasion of grasses and composites, such as occurred on the Tacoma "prairies" just south of Puget Sound (Hansen 1938). A decline in the pollen percentages of oak and a resumption of Douglas fir predominace to the uppermost horizon may mark a cooler and moister climate in more recent time.

A general decrease in moisture during the middle third of the post-Pleistocene is suggested by most of the pollen spectra of Pacific Northwest peat profiles, with the exception of those in proximity to Puget Sound. Some peat deposits, however, record more definitely a dry, warm period, succeeded by a slight increase in moisture in more recent time. In a bog near Spokane, Washington, located in a western yellow pine climax, a sharp increase in the proportions of grass, chenopod, and composite pollen about one-third the way upward in the profile signifies the occurrence of a hot, dry climate (Hansen 1939b). These species were later replaced by forests consisting largely of yellow pine, suggesting a return of a moister and cooler climate, which persisted to the present time. Lake sediments in the Upper Sonoran life zone of east central Washington record relative trends of forest and grassland succession that depict a gradual drying and warming to a maximum, followed by some cooling and greater precipitation (Hansen 1941e). Pollen analyses of four profiles of lake sediments from Lower Klamath Lake of southern Oregon and northern California also denote the development of a xeric period, followed with an increase in moisture (Hansen 1941g). The evidence offered by the pollen profiles is further corroborated by the occurrence of artifacts underlying from 6 to 8 feet of fibrous peat (Cressman 1940). The wide distribution of the artifacts over hundreds of square miles of the exposed fossil lake bed marks the drying up of the lake and the occupancy of the lake bed by early man between 7500 and 4000 years ago (Antevs 1940). The salinity of certain lakes in the Great Basin is also supporting evidence for the occurrence of a xeric period during the postglacial. The present salinity of these lakes is such as to have required not over 4000

years for its development (Antevs 1938). The lakes had their origin in the Pleistocene, dried up during the post-Pleistocene, and their precipitated salts were removed by deflation or buried. The present lakes were reformed in their freshened basins about 4000 years ago (Antevs 1940). The drying and reforming of these lakes seem to be closely correlated with the disappearance and rebirth of most of the western mountain glaciers. Evidence shows that the existing glaciers in the Sierras are not remnants of the Pleistocene glaciers, but those that came into existence only a few thousand years ago (Matthes 1939). Their recession and readvance apparently have been more or less synchronous with the drying and rebirth of the lakes of the Great Basin. Pollen profiles from eastern North America also designate a drying and warming to a maximum, followed by a somewhat cooler and moister climate (Smith 1940).

SUMMARY

Three profiles of lake sediments in the Lower Willamette Valley of western Oregon record an interesting and significant trend of post-Pleistocene forest succession by the forest tree pollen recorded therein. The depth and pollen spectra of the Onion Flat profile suggest that sedimentation was initiated in early post-Pleistocene, and that it records adjacent forest succession from the Pleistocene almost to the present. An unknown thickness of the upper sediments has been removed in all profiles, due to drainage and cultivation. The Onion Flat profile probably represents a longer period of time for its deposition than the Lake Labish profiles.

The earliest recorded forests of the Willamette Valley and adjacent slopes of the Coast and Cascade Ranges consisted largely of lodgepole pine, Sitka spruce, and lowland white fir. This is extremely significant, because the first two species are seemingly absent from the Willamette Valley at present. These initial postglacial forests were slowly replaced by Douglas fir, which in turn was replaced to some extent by white oak. Douglas fir shows a general increase upward in the profiles with white oak, which supersedes the former in the upper levels of the profiles. Oak declines to the top after it attained its maximum, and Douglas fir resumed its predominance to the uppermost level.

Climatically this trend of forest succession denotes a long period of moist conditions with considerable instability of the edaphic and physiographic conditions. The latter conditions are suggested by the persistence of lodgepole pine as indicated by the presence of its pollen in abundance in the lower two-thirds of the Onion Flat profile. As the influence of recent glaciation waned, the climate became warmer and drier, as is evidenced by the invasion of Douglas fir, followed by that of white oak. The xeric period reached its maximum during the period of oak predominance. The climate

became moister and cooler during the latter part of the postglacial. The small amount of western hemlock pollen in the profiles indicates that the initial edaphic and physiographic conditions were too rigorous for its existence, and later the climate became too dry for its development to any great extent. The evidence for this climatic trend is more definite in this study than that offered by other pollen profiles west of the Cascades. Evidence for a similar dry period is present in peat profiles east of the Cascades in Washington and Oregon. These climatic interpretations are also supported by anthropological and geological studies in the Great Basin.

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VEGETATIONAL STUDIES IN AREAS OF SEDIMENTATION IN THE BONNET CARRÉ FLOODWAY

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INTRODUCTION

The City of New Orleans was founded in 1718 "to secure the river and Louisiana against covetous Spain and England" (La. Writers Project, 1941). Ever since its founding, the city has been subject to the threat of recurrent floods. No comprehensive plan of levee construction, however, was begun until 1828, when a severe flood caused legislative action by the State of Louisiana (Russell 1936). Although much construction had been accomplished by 1882, the great flood of that year, sweeping through 284 crevasses and washing away 56 miles of levee, set the stage for a concerted campaign by the State and Federal governments to control the river. The levee system, however, again proved inadequate in 1927, at which time the levee at Caernarvon below New Orleans was dynamited to relieve flood pressure on the city. This resulted in further flood control projects such as storage reservoirs, cut-offs and artificial floodways.

One of these artificial floodways is the Bonnet Carré Floodway, located at a point some 20 miles upstream from the city of New Orleans. It has been constructed in an area where several natural crevasses have occurred. The most extensive of these, just above the site of the present floodway, was created when the artificial levee was breached on April 11, 1874. This crevasse remained open for almost nine years and built up an extensive area of alternating ridges and swales. This type of land surface is known as "Crevasse topography" and is plainly evident between the present floodway and the town of La Place.

The Bonnet Carré Floodway consists of a one-and-one-half-mile concrete weir (spillway), which fronts the river, and two guide levees which extend in a Northeasterly direction for a distance of about five-and-one-half miles to Lake Pontchartrain. It was first utilized in the winter of 1937 to relieve the pressure of the greatest controlled flood in the history of the Mississippi River. The spillway was opened on January 29, 1937, and remained open until March 17, 1937 (fig. 1). The passage of the flood waters resulted in

[1] The writers are indebted to the New Orleans District Office of the United States Army Engineers for permission to make studies in the floodway and for data concerning sedimentation. To Faith Pennebaker Mackaness, Tulane University, and Thomas F. Hall, Tennessee Valley Authority, for assistance on several field trips the authors express their gratitude. They are indebted also to Mrs. Agnes Chase who identified several grasses and to Dr. Henry K. Svenson for the identification of a number of perplexing sedges.

considerable deposition of alluvium. The sediments were deposited in a striking pattern of irregular sand ridges or dunes up to 14 feet in height. Since several natural crevasses have occurred in the immediate vicinity these deposits are superimposed, in part, on "crevasse topography" of former natural diversion channels.

FIG. 1. The spillway (right) was opened on January 27, 1937, to relieve flood pressure on the City of New Orleans. (Floodway at left.)

DISTRIBUTION AND COMPOSITION OF SEDIMENTS

The bulk of the alluvium was deposited near the spillway, because of the decreased carrying power of the flood waters occasioned by the very great change in the direction of the flow. Furthermore, low-growing groups of trees, shrubs, and vines augmented the deposit and increased the height of the ridges, especially on the lakeward side of the masses of vegetation.

Although the dunes included fine sand, silt, and clay, the coarser sediments predominated. Data supplied by the United States Army Engineers Office reveal the fact that the percentage of finer sediments increased gradually with the distance from the weir. It should be pointed out, however, that the sediments in areas of slight deposition, even though relatively close to the spillway, were much finer than the alluvium of the dunes and swales.

With the composition of the sediments in mind, stations were selected relatively near (1000–1500 feet) the spillway, adjacent to the airline highway (about 9000 feet from the spillway) and in an area of slight deposition

on the lakeward side of the airline highway. The components of the soil, as determined from surface samples, at these stations are much alike except at Station 3, which was located in an area of slight deposition.

	Per cent		
	Sand	Silt	Clay
Station 1 (near spillway)	93.3	3.4	3.3
Station 2 (near highway)	89.9	3.3	6.8
Station 3 (lakeward from highway)	2.9	69.6	27.5

Determinations of water content were made at all stations in May, August, and October, 1937. The content was least in August and highest in the month of October but was ample throughout the growing season. The unusually high soil moisture in October is in accord with the abnormal rainfall for that month (25.11 inches) which was 21.81 inches more than the long term average and the highest precipitation for any one month in the history of the New Orleans Weather Bureau. As might be anticipated, water content increased with the depth of the sample. Furthermore the percentage of water was greater at the same sample depth in the swales than on the ridges.

Fourteen determinations of the pH of the sediments were made by a La Motte-Morgan indicator set. These tests gave a pH range of 7.6 to 8.4 but did not indicate any correlation with topography, water content, or vegetation.

ORIGINAL VEGETATION

The original land surface in the floodway slopes gradually from the Mississippi River to Lake Pontchartrain about five-and-one-half miles to the northeast. The frontlands along the river are composed of coarser sediments and are better drained than the backlands. It is probable that the frontlands were clothed originally with a hardwood forest in which water oak, live oak, and hackberry were the predominant species. The much more extensive backlands were occupied by a swamp forest in which bald cypress and tupelo gum were the important dominants.

At the time the floodway was completed in 1935 the frontlands were largely in cultivation. But there were scattered water oaks, live oaks, hackberries, pecans, and sycamores, as well as numerous specimens of rough-leaved dogwood, poison ivy, pepper-vine, supple-jack, and trumpet-vine. The swamp forest, although completely cut over in the past, still presented a true forest aspect, with a fairly continuous stand of bald cypress, tupelo gum, and swamp maple.

EFFECT OF FLOODWAY OPERATIONS ON PREEXISTING VEGETATION

As far as could be ascertained the flood waters per se produced no observable deleterious effect on the former vegetation in the floodway. This was

true in spite of the fact that the water covered the soil to a considerable depth (several feet) for a period of more than 46 days (the period during which the spillway was open). The answer probably lies in the fact that the spillway was opened on January 29 before much plant activity had started. Furthermore, the relatively cold water in the floodway undoubtedly prolonged the dormancy of many species of woody plants.

On the other hand the alluvial deposits, especially those over one foot in thickness, killed nearly all herbaceous plants, a considerable number of shrubs, vines, and seedling trees, and a few sapling trees. In order to determine the percentage destruction of woody plants, ten temporary quadrats were established and studied in June and August. Individual shoots that projected through the alluvium were listed according to species, their diameter at the ground level in inches (d.g.l.) and their state of health. Since it was often impossible to determine whether a shoot represented an individual or merely a branch of a plant, each shoot was given equal rank in the averages. The shoots were listed as healthy, unhealthy, or dead. Typically, the leaves of unhealthy plants were yellowed or were browned from the edges inward. In the absence of leaves, the shoots were cut to determine whether they were living or dead.

On the whole, the healthy shoots far outnumbered the unhealthy and dead specimens in June. Of the 465 individual shoots examined in all habitats, 282 were healthy, 87 were sickly, and 96 were dead. On the ridges the proportion of healthy shoots was somewhat lower than it was in the swales. This suggests that the destruction varies directly with the thickness of the alluvium.

It was also found that the health of the woody plants varied directly with the d.g.l. of the shoots. This is well illustrated in the following table of four of the common species:

Species	Average d.g.l. (inches)	
	Healthy	Dead
Quercus virginiana[2]	1.94	0.40
Celtis mississippiensis	2.18	1.25
Hicoria pecan	2.16	0.40
Svida asperifolia	1.79	0.49

Of all the woody species the small shrubs exhibited the greatest mortality, whereas nearly all trees over 6 inches d.g.l. and most woody vines escaped destruction. Nearly all specimens of *Cerothamnus ceriferus, Rhus copallinum, Rubus* spp., and *Sambucus canadensis* observed had succumbed by the time of the June survey. On the other hand *Diospyros virginiana, Gleditsia triacanthos, Bignonia radicans,* and *Vitis* spp. exhibited no injury in June. In addition to the above species, no injured specimens of *Berchemia scan-*

[2] Plant nomenclature follows Small's *Manual of the Southeastern Flora.*

dens, Brunnichia cirrhosa, Celtis mississippiensis, Hicoria pecan, Ilex decidua, Platanus occidentalis, Quercus virginiana, Rufacer drummondii, or *Ulmus americana* were found in the autumn survey.

PIONEER VEGETATION

In our study of the revegetation of sediments, twelve plots at three widely separated stations were utilized. All these plots included ridges and swales in areas of considerable deposition as well as flats in an area of very slight alluviation. The vegetation was analyzed by phytosociological methods similar to those used by Penfound and Howard (1940) as modified from

2 3

FIG. 2. The feathery aspect of the Panicum associes is due to the witch grass, *Panicum capillare.* FIG. 3. In this example of the Cyperus-Panicum locies, *Panicum dichotomiflorum* is the predominant species.

Braun-Blanquet (1932). Each of the twelve plots was analyzed in June, August, and October of 1937. Similar analyses would have been made during the 1938 growing season had not the areas under investigation been drastically disturbed by clearing and by levelling of the dunes. Detailed phytosociological data are not presented in this paper owing to the exigence of space but will be made available to the reader upon request.

In general, it was found that the high and low ridges were occupied by a community which we have designated as the Panicum associes (fig. 2). Although the swales included several more hydric species than the ridges

we have designated the community found therein as the Cyperus-Panicum locies of the Panicum associes.

PANICUM ASSOCIES

In the spring survey the Panicum associes (on the ridges) was characterized by many species with a very low total coverage. The most important species at this time, in decreasing order of coverage comprised *Panicum capillare*, *Panicum dichotomiflorum*, *Digitaria sanguinalis*, *Cyperus esculentus*, *Mollugo verticillata*, *Eragrostis hypnoides*, and *Eragrostis pectinacea*. The first two of these species especially continued to increase in coverage throughout the season and are considered the community dominants. Of the total cover in the October survey over 70 per cent was contributed by *Panicum capillare* and about 10 per cent was occasioned by *P. dichotomiflorum*. The last four of the above species exhibited progressively lower coverage in the August and October surveys. This decline in importance as community components is probably due to their ephemeral habit. Calculation of total coverage, using the June survey as unity, gave the following relative values: June, 1; August, 1.7; October, 4.0.

The Panicum associes included a total of 102 species. Some of the species were encountered only in one or two of the surveys but the dominants were present throughout the growing season. As might be expected the number of species increased with the season (June, 73; August, 80; October, 85). Of the 102 species encountered 41.7 per cent were members of three families: Poaceae (18.4), Carduaceae (13.6), and Cyperaceae (9.6).

CYPERUS-PANICUM LOCIES

The alluvium in the swales varied from less than one foot to three feet in thickness and possessed a relatively high moisture content (20.4–52.4 per cent). Owing to the relatively high water content of the sediments, many hydric species developed which did not survive on the ridges. Despite the presence of these species it is felt that this community should be designated as a form of the Panicum associes, since 38 per cent of the total number of species and all of the dominant species were common to both communities (table 1).

TABLE 1

List of species encountered in plant communities developing on the deposits in the Bonnet Carré Floodway

A. Present in Panicum Associes only

Acalypha virginica	*Cerothamnus ceriferus*	*Diodia virginiana*
Ageratum conyzoides	*Chenopodium album*	*Dracopus amplexicaulis*
Ambrina ambrosioides	*Cirsium horridulum*	*Echinochloa crus-galli mitis*
Arundinaria tecta	*Croton capitatus*	*Eleusine indica*
Berchemia scandens	*Cynoctonum mitreola*	*Eragrostis spectabilis*
Bignonia radicans	*Cyperus* sp.	*Erigeron canadense*
Calyptocarpus vialis	*Digitaria sanguinalis*	*Fimbristylis diphylla*

Fraxinus americana
Heliotropium inundatum
Holcus halepensis
Ipomoea lacunosa
Iva ciliata
Leptilon canadense
Leptochloa uninerve
Maruta cotula
Medicago lupulina
Meibomia sp.
Mimosa strigillosa
Muhlenbergia schreberi
Paspalum conjugatum
Paspalum dilatatum
Paspalum urvillei
Persicaria hydropiper
Persicaria hydropiperoides
Persicaria sp.
Phyla nodiflora
Portulaca oleracea
Sambucus canadensis
Setaria lutescens
Sida carpinifolia
Sida rhombifolia
Sida spinosa
Solanum nigrum
Sporobolus cryptandrus
Strophostyles helvola
Svida asperifolia
Ulmus americana
Xanthoxalis micrantha
Xanthoxalis sp.

B. Common to Panicum associes and Cyperus-Panicum locies

Acnida tamariscina
Amaranthus deflexus
Ambrosia elatior
Ambrosia trifida
Ammannia coccinea
Ampelopsis arborea
Aster sp.
Bidens frondosa
Boehmeria cylindrica
Brunnichia cirrhosa
Chamaesyce humistrata
Cynodon dactylon
Cyperus erythrorhizos
Cyperus esculentus[b]
Cyperus filicinus microdontus
Cyperus inflexus
Cyperus virens Drummondii
Echinochloa colona
Equisetum robustum
Eragrostis hypnoides
Eragrostis pectinacea
Eupatorium capillifolium
Fimbristylis autumnalis
Fimbristylis vahlii
Fraxinus sp.
Ipomoea sp.
Leucospora multifida
Lythrum lanceolatum
Mikania scandens
Mollugo verticillata
Oenothera biennis
Panicum capillare[a]
Panicum dichotomiflorum[a, b]
Persicaria punctata
Phyla lanceolata
Platanus occidentalis
Pluchea petiolata
Polypremum procumbens
Populus balsamifera
Raimmania laciniata
Rynchospora corniculata
Salix longifolia
Salix nigra
Sesban Emerus
Spilanthes americana
Thyella tamnifolia
Verbena bonariensis
Verbesina alba
Xanthium sp.

C. Present in Cyperus-Panicum locies only

Celtis mississippiensis
Echinochloa Walteri
Ilysanthes inequalis
Juncus diffusissimus
Jussiaea decurrens
Jussiaea leptocarpa
Leptochola panicoides
Ludwigia glandulosa
Mimulus cylindrica
Paspalum repens
Phyllanthus carolinensis
Pontederia cordata
Rubus sp.
Rufacer Drummondii
Scirpus sp.
Toxicodendron sp.
Trachelospermum difforme
Typha latifolia

[a] Dominant in Panicum associes.
[b] Dominant in Cyperus-Panicum locies of Panicum associes.

The predominant species of the Cyperus-Panicum locies, in order of relative coverage in October, comprised *Panicum dichotomiflorum, Cyperus esculentus, Jussiaea leptocarpa, Typha latifolia, Salix* spp., and *Eragrostis hypnoides.* Of the above, the first two species contributed over 70 per cent of the total coverage in October and have been designated as the community dominants (fig. 3). As in the Panicum associes, there was a slight increase in the number of species as the season progressed (June, 49; August, 52; October, 63). A total of 67 species (table 1) was encountered in this community. Of this number, 37 per cent were members of three families (Poaceae, 13.7; Cyperaceae, 13.7; Carduaceae, 9.6).

COMPARISON OF SPECIES WITH PIONEERS OF OTHER SANDY DEPOSITS

The vegetation of the dune ridges in the floodway is not at all similar to that of the strand flora of the Gulf Coast. Of 21 species listed by Lowe (1921)

as occurring on sandy beaches in the state of Mississippi, only one was encountered in the floodway. In their study of Cat Island, Penfound and O'Neill (1934) include 54 herbaceous species in the three dune associations on Cat Island, Mississippi, but of these species only three were found on the floodway deposits. On the other hand, many plants developing on the floodway sediments have also been found on relatively barren areas on the river side of the artificial levees. Of the 43 species that Brown (1929) found in a bare area caused by the construction of a levee near Baton Rouge, 55 per cent were encountered in the Bonnet Carré floodway. On revegetating sandbars of the Mississippi River Davenport (1934) encountered a total of 62 species, of which 60 per cent were common to the floodway deposits.

The alluvium in the floodway was much finer than the strand deposits along the Gulf Coast but it is not known whether this difference is sufficient to account for the great diversity in vegetation. It should be pointed out, however, that the water content in coarse, sandy soils is often critically low. The pH of the floodway sediments was found to be relatively high (7.6 to 8.4) as compared with that of the strand deposits (6.0 to 7.2). A review of the literature suggests, however, that most species survive under pH differences as great as those between the alluvial and strand deposits. A further suggestion has been made that the weedy communities on the alluvial sediments are due primarily to water-borne seeds from upstream sources. Presumably the availability of migrules would explain the presence of these ruderal species. It is probable, however, that very few of these species could survive on the coarse sands of the strand and that water content and possibly pH may be important controlling factors in this habitat.

SUMMARY

1. The vegational changes which occurred in the Bonnet Carré Floodway, subsequent to its use in flood control during the late winter of 1937, are herein reported.

2. The diversion of flood waters through the floodway resulted in a striking depositional pattern of alternating ridges and swales, typical of "crevasse topography." The sediment consisted of fine sand with a small admixture of silt and clay.

3. The flood waters had no observable direct effect on the preëxisting vegetation but the sediments, especially where over one foot in depth, destroyed the herbaceous plants and much of the woody vegetation.

4. Vegetational studies, made in June, August, and October of 1937, revealed only one plant community and a wet phase of the same.

5. The Panicum associes, which develops on the ridges, was dominated by *Panicum capillare* and *Panicum dichotomiflorum* at the end of the growing season. The community included 102 species distributed largely in three families: Poaceae, Carduaceae, and Cyperaceae.

6. The Cyperus-Panicum locies, which develops in the swales, was dominated by *Cyperus esculentus* and *Panicum dichotomiflorum*. A total of 67 species was recorded, of which 37 per cent were members of the Poaceae, Carduaceae, and Cyperaceae.

7. The pioneer vegetation of the floodway deposits is very unlike that of the strand flora of the Gulf Coast but quite similar to that of the sandbars of the Mississippi River.

FISH AND WILDLIFE SERVICE[3]
AND
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NEW ORLEANS, LOUISIANA

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[3] Investigation completed at Tulane University.

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THE GENUS CEPHALOCARPUS NEES (CYPERACEAE)

CHARLES L. GILLY

INTRODUCTION

Generic endemism in the tribe Lagenocarpeae is strikingly represented in the Sierra Pacaraima region of northern South America. The genus *Everardia* (4), the genus *Didymiandrum* (5), and the related genus *Cephalocarpus* have their center of distribution on this mountain complex, and the genus *Trilepis*—whose main distribution is in the similarly old mountainous region around Rio de Janeiro and in southern Minas Geraes—is represented by a single disjunct station in the Kanukus, an eastern outlier of the Pacaraima complex. These small genera are of interest because of the age of the area in which they are found, and because they exhibit certain characteristics which may be regarded as distinctly primitive within this family. Investigations which were begun while identifying Mr. G. H. H. Tate's Auyan-tepui[1] specimens of Cyperaceae (3) are continued in this paper.

The genus *Cephalocarpus*, established by Nees in the Flora Brasiliensis (7) with a single species *C. dracaenula*, has been merged with *Cryptangium* by Böckeler (1) and with *Lagenocarpus* by Pfeiffer (9); neither of these treatments, however, is acceptable on the basis of a study of the more recently collected material. Clarke (2) accepted Böckeler's merger, but other botanists who have worked with the Cyperaceae have usually recognized *Cephalocarpus* as a distinct genus.

In 1921 (8), when placing *Cryptangium* in synonymy under *Lagenocarpus*, Pfeiffer removed Böckeler's *Cryptangium dracaenula* (based on *Cephalocarpus dracaenula* Nees) from the enlarged and emended genus as "*Cephaloscirpus* [sic!] *Dracaenula* Nees," thereby recognizing *Cephalocarpus* as distinct. Then, in 1922 (9), he reduced the genus to subgeneric status under *Lagenocarpus;* in this new subgenus he placed *L. polyphyllus* Kuntze, *L. clarkei* H. Pfeiff. (nom. nov. for *Cryptangium strictum* C. B. Clarke), *L. humilis* Kuntze, and *L. comatus* H. Pfeiff. The only apparent basis for such inclusion seems to be the anomalous and dissimilar habits of these four species which are as unlike each other as they are unlike *C. dracaenula* in appearance. Inflorescence, spikelet, and achene characters of these species certainly do not indicate such close relationship as Pfeiffer would infer. On page 72 of the same paper, "*for the convenience of those*

[1] "Tepui," an Indian dialect name, means "mountain"; thus, Auyan-tepui is, in reality, Mt. Auyan. Mt. Roraima is known by the natives of the region as Roraima-tepui, and Mt. Duida as Duida-tepui.

who are inclined to accept smaller genera,"[2] he makes the combinations *Cephalocarpus comatus, C. humilis, C. polyphyllus,* and *C. clarkei.* The last of these needlessly created combinations was, incidentally, improperly made, for it was based on *Cryptangium strictum* C. B. Clarke; while the specific epithet *strictus* had already been used in the genus *Lagenocarpus,* thus necessitating a new name for the species in that genus, it had not been used in *Cephalocarpus.* In 1924 (10) Pfeiffer added another anomalous species, *L.* (*Cephalocarpus*) *schenckianus* H. Pfeiff., to the subgenus *Cephalocarpus.*

The five species transferred to his new subgenus by Pfeiffer are untenable in *Cephalocarpus* Nees (see list of excluded species at end of this paper); whether they may be retained in *Lagenocarpus,* or whether they must be referred to the genera under which they were originally described, is not a matter for consideration in the present paper.

Cephalocarpus, then, has remained as a monotypic genus for almost one hundred years. While studying the Tate collections of Cyperaceae from Mt. Roraima, Mt. Duida, and Auyan-tepui, I discovered that certain specimens, provisionally referred to the genus "*Everhardia*" by Dr. Britton in the report on the flora of Mt. Duida (6), represented undescribed species of *Cephalocarpus.* At the time I published *C. rigidus* and *C. longibracteatus* in the Auyan-tepui report (3), I had not examined the type of *C. dracaenula* Nees; hence, on page 153 of that paper, I stated, "It is of interest to note that *C. Dracaenula* has been collected on both Mt. Roraima (*Tate 285*), and Mt. Duida (*Tate 800*)." This statement was made because I had provisionally associated these two specimens with Nees' original description and plate (7). My recent discovery—in the Gray Herbarium—of a specimen which is undoubtedly an isotype of the Nees species, has shown without question that *Tate 285* and *800* cannot be referred to *C. dracaenula.* Further study indicates that *Tate 720* and *721,* which I referred (3) to *C. rigidus,* can scarcely be regarded as conspecific with *Tate 1346* and must therefore be considered as a distinct entity. Another specimen, *Tate 1035,* in the herbarium of the New York Botanical Garden, proves also to be specifically distinct.

Cephalocarpus should be referred to the tribe Lagenocarpeae,[3] and appears to be most nearly related to the genus *Evarardia.* From this genus, which has elongated and compound inflorescences, achenes which taper into conical beaks, and 6 stamens subtended by each staminiferous glume, *Cephalocarpus* differs in having capitate-condensed inflorescences, achenes with clavate beaks and 2–3 stamens subtended by each staminiferous glume.

[2] ". . . ut iis, qui parva genera anteponunt, genus solutum Cephalocarpus discernendae sint."

[3] This tribe is usually called the Cryptangieae, but because of the doubtful status of the genus *Cryptangium* I am following Pfeiffer in the choice of a tribal name.

From *Lagenocarpus*, which has terminal inflorescences and lacks a perianth, *Cephalocarpus* differs in having axillary inflorescences and a definite perianth.

With one exception, the distribution of *Cephalocarpus* parallels that of *Everardia* (4), both genera having been collected from Auyan-tepui, Mt. Duida, and Mt. Roraima of the Sierra Pacaraima complex. In addition to these localities *Cephalocarpus* has been found in the Cupati Mountains (the generic type locality), a low range of foot-hills geologically similar to the Pacaraimas, near the Caqueta (= the upper Japuru) River in what is now eastern Colombia.

I wish to thank Dr. J. H. Barnhart for bibliographical assistance, and Dr. C. A. Weatherby for the loan of a specimen and type photographs which are deposited in the Gray Herbarium.

TAXONOMIC TREATMENT[4]

CEPHALOCARPUS Nees, in Mart. Fl. Bras. **2** (1): 162, *t. 18*. 1842.

Lagenocarpus, subgenus *Cephalocarpus* H. Pfeiff. Repert. Spec. Nov. **18**: 91. 1922.

Terrestrial or epiphytic perennials. Stems rhizomatous, woody, simple or branched, surrounded by the persistent and more-or-less ragged sheaths of previous years' leaves and partially supported by prop-roots. Leaves linear, acute, somewhat flattened below, bicarinate above, crowded at apices of stem or its branches, 3-ranked but sometimes so closely crowded as to appear many-ranked. Flowering culms axillary, solitary and basally enclosed by a sheath, or 3–8 together and all basally enclosed by a single sheath; basal sheaths (prophyllons) membranous, 2-keeled, bifid by the prolongation of the keels beyond the tubular portion. Inflorescences of simple or compound capitate clusters of monoecious spikelets subtended by 2–several leaf-like bracts, the inflorescences usually containing both kinds of spikelets or some of them composed wholly of staminate spikelets. Spikelets sessile or short-pediceled, the pedicels basally bracteolate by 1–4 minute, hyaline, nerveless, acute or bifid scales. Staminate spikelets 2–5-flowered; empty outer glumes 2–5, staminiferous inner glumes 2–7, sometimes 1 or 2 of the innermost empty; stamens subtended by each staminiferous glume 2 (or rarely 1 or 3); filaments flattened, exserted, persistent; anthers linear, basifixed, 2-celled, the connective prolonged between the thecae into a minute pubescent mucro. Pistillate spikelets usually fewer in number than the staminate, 1-flowered, the ovary surrounded by 4–6 spirally imbricated glumes; rarely (and abnormally) the second or third glume subtends a single staminate flower. Achenes terete to obtusely triangular, obovoid, more or less conspicuously marked by 3 longitudinal tricarpellary lines, the apex depressed and centrally apiculate, the apiculation covered by a clavate, pubescent or glabrous, persistent or tardily deciduous beak formed by a prolongation of the outer pericarp layer. Style short, deciduous; stigmas 3, terete, linear, elongated, exserted; both style and stigmas densely and mi-

[4] Specimens examined in the preparation of this paper are deposited in the herbarium of the New York Botanical Garden (NY), and in the Gray Herbarium (GH).

nutely glandular-pubescent. Perianth cupular, usually persistent on the base of the achene, formed by partial marginal fusion of 3 minute ciliate-margined hypogynous scales.

TYPE SPECIES: *Cephalocarpus dracaenula* Nees.

KEY TO THE SPECIES

Flowering culms 3–8 together in the axil of a single leaf, all basally enclosed within a single tubular sheath; beak of achene tardily deciduous, exposing the terminal apiculation of the achene body (Subgenus 1. *Eucephalocarpus*[5]).

Beak of achene glabrous, shining, yellow, the body bright reddish-brown; perianth scales orbicular; leaves thinly white-pilose on the margins ..... 1. *C. confertus*

Beak of achene pubescent, both beak and body dull, stramineous; perianth scales acutely triangular; leaves coarsely ciliate at base, the margins above minutely scabrous ..... 2. *C. dracaenula*

Flowering culms solitary in the leaf axils, each enclosed by a basal tubular sheath; beak of achene persistent, permanently attached to and covering the terminal apiculation of the achene body (Subgenus 2. *Neocephalocarpus*[6]).

Leaves flexible, less than 1.5 mm. in width, 8–15 cm. long; achenes 0.75 mm. in diam. ..... 3. *C. linearifolius*

Leaves rigid, 1.5 mm. or more in width, less than 8 cm. long; achenes 1–1.5 mm. in diam.

Inflorescences simply-captitate; lowest bract subtending the inflorescence less than 10 mm. long, its sheath glabrous or finely appressed-pubescent, the margins of the free portion appressed-pubescent or scabrid.

Outer glumes of spikelets bifid at apices, their midribs prolonged between the teeth into prominent scabrid mucros; leaf margins scabrid ..... 4a. *C. rigidus* var. *typicus*

Outer glumes of spikelets tapering gradually into the acute or mucronate apices, never bifid; leaf margins and midrib beneath appressed-pubescent ..... 4b. *C. rigidus* var. *mucronatus*

Inflorescences compound-capitate; lowest bract subtending the inflorescence 10–25 mm. long, its sheath densely white-villous, the margins of the free portion pilose ..... 5. *C. longibracteatus*

SUBGENUS 1. EUCEPHALOCARPUS GILLY.

1. **Cephalocarpus confertus** Gilly, sp. nov.

Rhizomata crassa ramosa, ad 5 cm. alta: folia valde conferta, late linearia acuta bicarinata, 3–7 cm. longa, 2–3.5 mm. lata, glabra margine et costa albo-villosa exceptis; culmi floriferi ad 1.5 cm. longi, 3–5 aggregati in axillibus foliorum; bracteae inflorescentiam subtendentes 2–4, inferiores 4–7 mm. longae; spiculae masculae 4–6 mm. longae, 0.75–1 mm. diam., glumis vacuis lanceolatis acutis glabris, glumis fertilibus oblongis acutis hyalinis; spiculae foemineae masculas aequantes, glumis 4–5, lanceolatis acutis vel mucronatis; achaenia subteretia obovoidea glabra rubro-brunnea, 1.25–1.5 mm. longa,

[5] **Eucephalocarpus** Gilly, subgen. nov. Culmi floriferi 3–8 aggregati axillibus foliorum; rostro subpersistente, deciduus ad ultimum apiculus achaenium expositio. Subgeneris typus: *Cephalocarpus dracaenula* Nees.

[6] **Neocephalocarpus** Gilly, subgen. nov. Culmi floriferi solitarii axillibus foliorum; rostro persistente; apiculus achaenium obscurus. Subgeneris typus: *Cephalocarpus rigidus* Gilly.

0.75 mm. diam., rostro clavato glabro luteo subpersistente, 0.75–1 mm. longo, apiculo 0.7 mm. longo; squamellae hypogynae orbiculares, pilis paucis squamellas aequantibus.

In this species the second or third glume of the pistillate spikelet rarely (and apparently abnormally) subtends a single staminate flower.

TYPE: VENEZUELA—TERRITORIO AMAZONAS: Mount Duida, dry ridge tops, Savanna Hills, Alt. 4400 ft., Aug. 1928–Apr. 1929, *Tate 800* (NY). Also examined: VENEZUELA—BOLIVAR: Mount Roraima, on the great sand-stone boulders, Philipp Camp, alt. 5200–6000 ft., Nov. 7, 1927, *Tate 285* (NY).

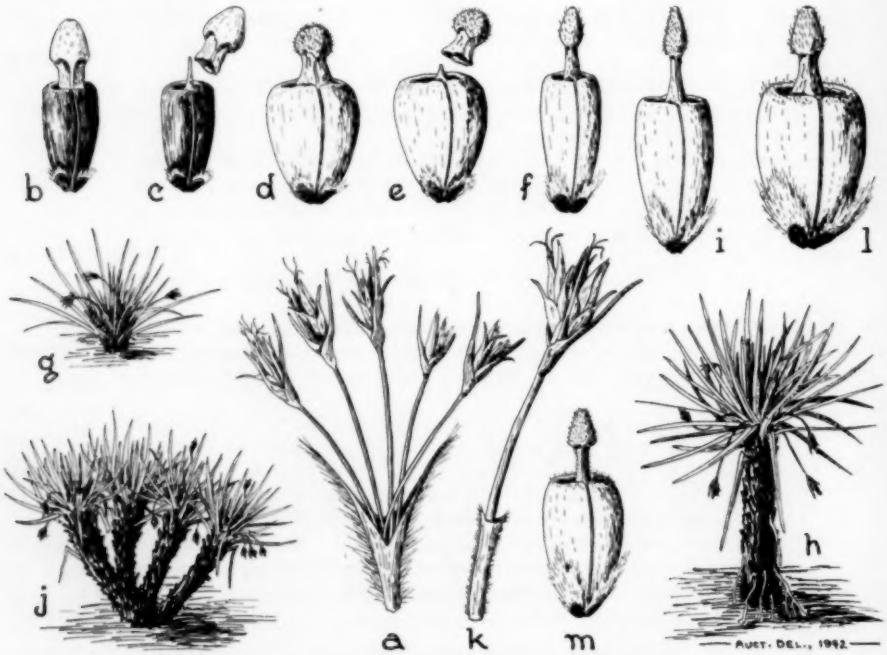

FIG. 1. *Cephalocarpus:* habit sketches ×0.5; flowering culms ×2.5; achenes ×5. *C. confertus* Gilly (drawn from *Tate 800*): *a*, aggregated flowering culms surrounded by a single basal sheath, characteristic of the subgenus *Eucephalocarpus; b*, achene, beak attached; *c*, achene, beak detached. *C. dracaenula* Nees (drawn from *Martius s.n.*): *d*, achene, beak attached; *e*, achene, beak detached. *C. linearifolius* Gilly (drawn from *Tate 1035*): *f*, achene. *C. rigidus* var. *typicus* Gilly (drawn from *Tate 1346*): *g*, young plant, the rhizome not yet evident above ground; *h*, old plant, showing well developed rhizome; *i*, achene. *C. rigidus* var. *mucronatus* Gilly (drawn from *Tate 720*): *j*, old plant, showing branched aerial rhizome; *k*, solitary flowering culm enclosed by basal sheath, characteristic of the subgenus *Neocephalocarpus; l*, achene. *C. longibracteatus* Gilly (drawn from *Tate 1345*): *m*, achene.

2. CEPHALOCARPUS DRACAENULA Nees, in Mart. Fl. Bras. **2** (1): 162. *t. 18.* 1842. *Cryptangium dracaenula* Böckl. Linnaea **38**: 415. 1874. *Lagenocarpus dracaenula* H. Pfeiff. Repert. Spec. Nov. **18**: 92. 1922.

Rhizome slender, to at least 30 cm. tall, simple or branched. Leaves loosely clustered, rigid and more or less erect, 2–3 mm. wide, 7–8 cm. long, coarsely ciliate at mouth of sheaths, otherwise glabrous except for scabrous margins

and under surface of midrib. Flowering culms 4–8 together in the axil of a single leaf, flattened with scabridulous margins; basal sheath 1.5 cm. long, deeply bifid at the apex. Bracts subtending the inflorescence 2–3, glabrous except for the coarsely ciliate margins of the free portions, the lowermost 5–6 mm. long. Staminate spikelets 5 mm. long, about 1 mm. in diam.; sterile glumes 2–4, broadly lanceolate, abruptly tapering into a prominent mucro; fertile glumes 3–5, lanceolate, acute, the midrib obsolete. Pistillate spikelets 5 mm. long, 1–1.5 mm. in diam., glumes 5–6, narrowly ovate to lanceolate, glabrous, mucronate, mucronulate, or acute, the mucro of the outermost sometimes coarsely ciliate. Achene stramineous, the body 1.5 mm. long, 1.25 mm. in diam., obovoid, subterete, glabrous except for the sparse pubescence at the apex. Beak about 0.75 mm. long, the apical knob hemispherical, pubescent; the beak tardily deciduous, thus exposing the 0.2–0.3 mm. apiculation in the center of the depressed apex of the achene body. Style 2–3 mm. long; stigmas 3 mm. or less in length, dark red-brown. Hypogynous scales triangular, acute, the marginal hairs sparse, about 0.3 mm. long.

Specimen examined: COLOMBIA—CAQUETA: [Cupati Mts.] cataracts of the Rio Japuru (=Rio Caqueta), 1841, *Martius s.n.* (GH). This specimen is an isotype.

SUBGENUS 2. NEOCEPHALOCARPUS GILLY.

3. **Cephalocarpus lineariifolius** Gilly, sp. nov.

Rhizomata gracilia simplicia vel ramosa, ad 15 cm. alta; folia linearia acuta bicarinata glabra margine et costa appresso-pubescentibus exceptis, 8–15 cm. longa, 1.5 mm. lata minusve; culmi floriferi solitarii in axillibus foliorum, 6–8 cm. alti; bracteae inflorescentiam subtendentes 10 mm. longae; spiculae masculae 3.5–5 mm. longae, glumis sterilibus 2–3, lanceolatis acutis; antherae 1–1.25 mm. longae; spiculae foemineae 4–5 mm. longae, glumis 4–5, lanceolatis acutis vel mucronatis marginibus et mucrone pubescentibus; achaenia subteretia obovoidea glabra straminea, 1.75–2 mm. longa, 0.75 mm. diam., rostro stramineo persistente glabrato vel vix pubescente, 0.75–1 mm. longo; squamellae hypogynae suborbiculares, ciliis subcopiosis quam corpore achaenii 3–plo brevioribus.

TYPE: VENEZUELA—TERRITORIO AMAZONAS: Mount Duida, flat near stream at Central Camp, epiphytic on bark of trees, alt. 4800 ft., Dec. 20–28, 1928, *Tate 1035* (NY).

4. CEPHALOCARPUS RIGIDUS Gilly apud Gleason & Killip, Brittonia **3**: 152. 1939.

In the report on the flora of Auyan-tepui (3), I referred two specimens from Mt. Duida to *C. rigidus;* further study of these specimens indicates that they can scarcely be regarded as conspecific with *Tate 1346* (the type of *C. rigidus*) from Auyan-tepui, and it therefore becomes necessary to describe them as a separate entity. However, from the specimens available I do not feel justified in recognizing the Duida material as a distinct species and so—for the present—it seems better to regard *C. rigidus* as a collective species composed of two geographically isolated varieties. Since the illustrations of the glumes (l.c., *fig. 2; a, b*) do not represent the typical form of the species, and since the original description of *C. rigidus* combines the characters of both varieties, it seems necessary to here describe and differentiate these varieties.

4a. CEPHALOCARPUS RIGIDUS Gilly var. **typicus** Gilly, var. nov. *Cephalocarpus rigidus* Gilly apud Gleason & Killip, Brittonia **3**: 152. *fig. 2, c.* (as to type, but not as to description). 1939.

Rhizomata simplicia, ad 6 cm. alta; folia valde conferta rigida coriacea glabra margine scabra excepta, ad 2 mm. lata, 3–4 cm. longa; culmi floriferi solitarii in axillibus foliorum, 2–3 cm. alti; spiculae masculae ad 4 mm. longae, glumis sterilibus 3–5 ovatis vel lanceolatis bifidis aristatis vel mucronatis, glumis fertilibus 3–4 oblongis vel lanceolatis acutis hyalinis; spiculae foemineae 4.5–6 mm. longae, glumis 5–6 lanceolatis bifidis hyalinis aristatis vel mucronatis, apicibus pubescentibus; achaenia subteretia obovoidea glabra vel ad apicem pubescentia, 1.75–2 mm. longa, ad 1 mm. diam., rostro pubescente persistente stramineo, 1.25 mm. longo; squamellae hypogynae orbiculares, ciliis copiosis quam corpore achaenii 3– vel 2–plo brevioribus.

TYPE: VENEZUELA—BOLIVAR: Auyan-tepui, 2200 m., Dec. 1937, *Tate 1346* (NY).

4b. CEPHALOCARPUS RIGIDUS Gilly var. **mucronatus** Gilly, var. nov. *C. rigidus* Gilly apud Gleason & Killip, Brittonia **3**: 152. *fig. 2, a, b.* (in part, but not as to type). 1939.

Rhizomata simplicia vel ramosa, ad 6 cm. alta; folia 2–8 cm. longa, 2–2.5 mm. lata, glabra marginibus et costa appresso-pubescentibus exceptis; culmi floriferi solitarii in axillibus foliorum, 2–3.5 cm. alti, ad basim pilosi; bracteae inflorescentiam subtendentes 5–9 mm. longae; spiculae masculae 5–6 mm. longae, glumis vacuis 3–5, lanceolatis mucronatis, glumis fertilibus 3–4, lanceolatis hyalinis mucronulatis vel acutis; antherae 3 mm. longae; spiculae foemineae ad 5 mm. longae, glumis 4–6, ovatis vel lanceolatis aristatis; achaenia teretia obovoidea, 2 mm. longa, ad 1.5 mm. diam.; rostro 1–1.25 mm. longo persistente pubescente; squamellae hypogynae suborbiculares, ciliis copiosis quam corpore achaenii 3–plo brevioribus.

TYPE: VENEZUELA—TERRITORIO AMAZONAS: Mt. Duida, on soil, Ridge 16, 6800 ft., 1928–1929, *Tate 721* (NY). Also examined: from the same locality, a dwarfed form growing on rock, *Tate 720* (NY).

5. CEPHALOCARPUS LONGIBRACTEATUS Gilly apud Gleason & Killip, Brittonia **3**: 153. *fig. 2, d–f.* 1939.

Rhizome short, simple or branched. Leaves loosely clustered, 2–3.5 mm. wide, 4–8 cm. long, pale green, firm but not coriaceous, sparsely to densely pubescent. Flowering culms solitary in leaf-axils, flattened, 0.5–1 mm. wide, densely pilose at base, glabrate above, exserted 4–7 cm. from the sheath of the subtending leaf; basal sheath 1–1.5 cm. long, minutely and bluntly bifid at the apex. Inflorescence compound, consisting of several pedicellate spikelets and several pedicellate spikelet clusters, the whole subtended by 2–3 leaf-like bracts; lowermost bract 10–25 mm. long, others smaller, sheaths of all densely white-villous, margins of the free portions long-pilose; bracts subtending the individual spikelet clusters similar but smaller. Staminate spikelets 4.5–6 mm. long, 0.75–1 mm. diam.; sterile glumes 3–4, broadly lanceolate, hyaline except for the prominent midrib, acute to mucronate; fertile glumes 2–3, oblong to narrowly lanceolate, acute, hyaline. Pistillate spikelets 4–5 mm. long, 1–1.5 mm. in diam.; glumes 5–6, the outer broadly

lanceolate, abruptly aristate, the inner lanceolate, acute. Achene straw-colored, the body 1.6–1.8 mm. long, 1–1.3 mm. in diam., minutely pubescent at the apex; beak persistent, about 1 mm. long, densely apically pubescent. Hypogynous perianth scales orbicular; marginal cilia copious, one-third to one-half as long as the body of the achene.

TYPE: VENEZUELA—BOLIVAR: Auyan-tepui, 2200 m., Dec. 1937, *Tate 1345* (NY).

SPECIES EXCLUDED FROM THE GENUS

1. *Cephalocarpus clarkei* H. Pfeiff. Repert. Spec. Nov. **18**: 72. 1922. = *Cryptangium strictum* C. B. Clarke, Kew Bull. Add. Ser. **8**: 66. 1908. (*Lagenocarpus clarkei* H. Pfeiff. Repert. Spec. Nov. **18**: 92. 1922. Not *Lagenocarpus strictus* Kuntze, Rev. Gen. 754. 1891).

2. *Cephalocarpus comatus* (Böckl.) H. Pfeiff. Repert. Spec. Nov. **18**: 72. 1922. = *Cryptangium comatum* Böckl. Flora **65**: 351. 1882. (*Lagenocarpus comatus* H. Pfeiff. Ber. Deuts. Bot. Ges. **39**: 131. 1921).

3. *Cephalocarpus humilis* (Nees) H. Pfeiff. Repert. Spec. Nov. **18**: 72. 1922. = *Acrocarpus humilis* Nees, in Mart. Fl. Bras. **2** (1): 161. 1842. (*Lagenocarpus humilis* Kuntze, Rev. Gen. 754. 1891).

4. *Cephalocarpus polyphyllus* (Nees) H. Pfeiff. Repert. Spec. Nov. **18**: 72. 1922. = *Acrocarpus polyphyllus* Nees, in Mart. Fl. Bras. **2** (1): 160. 1842. (*Lagenocarpus polyphyllus* Kuntze, Rev. Gen. 754. 1891).

5. *Cephalocarpus schenckianus* (Böckl.) H. Pfeiff. Repert. Spec. Nov. **20**: 44. 1924. = *Cryptangium schenckianum* Böckl. Cyp. Nov. **2**: 27. 1890. (*Lagenocarpus schenckianus* H. Pfeiff. Ber. Deuts. Bot. Ges. **39**: 132. 1921).

THE NEW YORK BOTANICAL GARDEN,
NEW YORK, NEW YORK.

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10. ————. Additamenta ad cognitionem generis *Lagenocarpus*, IV. Repert. Spec. Nov. **20**: 42–45. 1924.

BULLETIN OF THE TORREY BOTANICAL CLUB
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NORTH AMERICAN RANUNCULI—IV

LYMAN BENSON

The first and second articles in this series of five (Bull. Torrey Club **68** (3, 7): 157–172, 477–490. 1941) deal with the subgenus *Euranunculus*, section *Chrysanthe*, and the third (Bull. Torrey Club **68**: 640–659. 1941) is a treatment of the sections *Echinella* and *Epirotes*. In this paper the sections *Flammula* and *Hecatonia* are discussed, concluding the subgenus *Euranunculus*. The present delimitation of subgenera and sections was published in an article entitled "The North American subdivisions of *Ranunculus*" (Am. Jour. Bot. **27** (9): 799–807. 1940). Detailed specific descriptions are reserved of the North American Flora.

SECT. 4. FLAMMULA (WEBB) L. BENSON

Perennials; achenes 1.2–3.2 mm. long, the beaks 0.3–1.5 mm. long or in typical *R. Flammula* 0.1–0.2 mm. long; petals 5–10, conspicuous and usually large, longer than the sepals, except in *R. oresterus*.

Nectary scale ciliate along the distal margin, the adjacent surface of the petal with some hairs; achenes about 3–3.2 mm. long; receptacle short-pubescent; achenes pubescent, each with a flat, winged stalk; stems scapose ..... 48. *R. Collomae.*

Nectary scale glabrous, the petal also glabrous; achenes 1.2–2.5 mm. long; receptacle glabrous except sometimes in *Ranunculus Populago;* achenes glabrous except in *Ranunculus alismaefolius* var. *Lemmonii*, never stalked.

Roots not with light-colored, fusiform, thickened storage regions at the bases.

Stems never rooting.

Roots glabrous in their mature portions; petals 6–16 mm. long, 3–8 mm. broad, exceeding the speals, obovate or in var. *montanus*, which has almost always 10 petals, oblanceolate or narrowly oblong and 2–3 mm. broad; basal leaf not broadest at the middle and tapering to the acute ends ..... 49. *R. alismaefolius.*

Roots densely and finely canescent their whole length; petals not exceeding the sepals, narrowly oblong, 3–5 mm. long, 1–2 mm. broad, always 5; basal leaf broadest at the middle and tapering to the acute ends ..... 50. *R. oresterus.*

Stems rooting adventitiously at at least the lower nodes (rarely not rooting in typical *R. Flammula*, which is restricted to Newfoundland and Nova Scotia).

Achene body about 2 mm. long, nearly rectangular, the beak 1.1–1.3 mm. long; stem 5–10 dm. long, 5–8 mm. in diameter at the base, rooting at only the lower nodes, the distal portion ascending ..... 51. *R. ambigens.*

Achene body 1.3–1.7 mm. long, obovate, the beak 0.1–0.8 mm. long.

Cauline leaves lanceolate, oblanceolate, or linear ..... 52. *R. Flammula.*

Cauline leaves ovate, ovate-lanceolate, or rarely subcordate.
Cauline petioles sheathing the stem; stem filiform, never fistulous ..... 52C. *R. Flammula* var.
Cauline petioles not sheathing the stem; stem often fistulous ..... 53. *R. hydrocharoides.*
Roots each with a small, light-colored, fusiform-thickened storage region at the base, this structure 1–2 mm. in diameter.
Stems rooting adventitiously at the nodes; leaves alternate, the flowers never in cymes ..... 54. *R. Gormanii.*
Stems never rooting; leaves commonly opposite, the flowers usually in cymes ..... 55. *R. Populago.*
Annuals; achenes 0.6–1 or rarely 1.5 mm. long, the beaks 0.1–0.2 mm. long.
Petals 5–9, large and conspicuous, about twice as long as the sepals; styles in anthesis 0.5 mm. long, filiform, deciduous in fruit; head of achenes hemispherical or ovoid ..... 56. *R. laxicaulis.*
Petals 1–3, minute and inconspicuous, shorter than or equal to the sepals; styles in anthesis 0.1–0.2 mm. long.
Sepals 5; upper cauline leaves linear to lanceolate or oblanceolate or very narrowly elliptic, sessile; achenes oblong-obovate, 0.6–1 mm. long, smooth, reticulate, or papillate, the units of the reticulate pattern perhaps 0.03 mm. in diameter when visible ..... 57. *R. pusillus.*
Sepals 3; upper cauline leaves ovate, petioled; achenes obovate, about 1.5 mm. long, reticulate, the units of the pattern about 0.1 mm. in diameter ..... 58. *R. alveolatus.*

48. **Ranunculus Collomae** L. Benson, sp. nov. Glabrous terrestrial perennials; roots 6–10, remarkably stout, 2–3 mm. in diameter; stems scapose, prostrate or ascending, not rooting adventitiously, 3–5 cm. long up to the lowest pedicel, 1.5–2.5 mm. in diameter, 1–3-flowered; radical leaf blades simple, oblanceolate to obovate, 2.5–5 cm. long, 0.8–1.5 or 2 cm. broad, entire, proximally attenuate and distally acute; petioles 2.5–3.5 cm. long; stipular leaf bases 1–1.5 cm. long, cauline leaves 1–3, opposite or alternate, lanceolate to oblanceolate, sessile; pedicels 2–5.5 cm. long in flower and 6–10 cm. long in fruit, glabrous; sepals 5, yellowish-green tinged with purple, spreading, elliptic, 5 mm. long, 3 mm. broad, pilose dorsally, about half the length of the petals, promptly deciduous; petals 5, yellow, obovate, 7–12 mm. long, 5–7 mm. broad, the nectary scale forming a pocket, broadly oblong, ciliate on the distal margin; stamens about 40–50; achenes 50–100 in an ovoid head 10–12 mm. long, 9–10 mm. in diameter, each achene obovoid, 3–3.2 mm. long, 2–2.2 mm. dorsoventrally. 1–1.2 mm. laterally, smooth, finely pubescent, the margin conspicuous, the achene beak slender, 1 mm. long, apically curved or recurved; receptacle ovoid-cylindrical, 1–2 mm. long in flower, 8–9.5 mm. long in fruit, finely pubescent.

Herba terrestris perennis glabra; radicibus 2–3 mm. diametro; caulibus non e nodis radicantibus, scaposis, 1 dm. longis, 1.5–2.5 mm. diametro, 1–3-floris; foliis oblanceolatis vel obovatis, integris, 2.5–5 cm. longis, 0.8–1.5 rariter 2 cm. latis; petiolis 2.5–3.5 cm. longis; petalis 5, flavis, obovatis, 7–12 mm. longis, 5–7 mm. latis; nectarii squamulis ciliatis, oblongis, latere non liberis; carpellorum capitulo ovoide, 10–12 mm. longo, 9–10 mm. diametro; acheniis 40–50, obovoidis, canescentibus, 3–3.2 mm. longis, rostro 1 mm. longo, curvato vel recurvato; receptaculo ovoide, 8–9.5 mm. longo, canescente.

Open, dry ground under yellow pines at 2,300–2,500 meters elevation; La Sal Mountains, southeastern Utah to Coconino County, Arizona. Western pine forest. April.

Type collection: near Bugglen (Buglan) Hill, South Rim of the Grand Canyon, Coconino County, Arizona: coll. April 10, 1941, *Mrs. Rose E. Collom 999*. TYPE in the Herbarium of the University of Arizona. ISOTYPE, B.

Significant specimens: UTAH: 20 miles west of Blanding, La Sal Mountains, *Harrison & Williams 5984*, *UA*, Utah[1]; ARIZONA: Jacobs Lake, Kaibab Forest, *Maguire 13550*, UA, Utah; South rim of Grand Canyon at Bugglen (Buglan) Hill, *Collom BHI*, May 8, 1940, *US*, *999*, April 10, 1941, *UA*, *B;* 1½ miles north of Foxburrow (Foxborough) Ranch, on Schnably Hill Road, Oak Creek Canyon, *Wetherill 1*, April 7, 1940, *UA*, *MNA*[1], *B*.

This species has affinity to *Ranunculus glaberrimus* Hook. var. *ellipticus* Greene, and in some respects it is a connecting link between the sections *Epirotes* and *Flammula* although it is definitely in the latter section. The following characters show relationship to var. *ellipticus:* (1) presence of only 6–10 large, coarse roots, (2) habitat in dry soil, (3) pubescent achenes, (4) winged stipe of the achene, (5) ciliate nectary scale (ciliate or glabrous in *R. glaberrimus*). Only four species of *Ranunculus* in North America have ciliate nectary scales. They are *R. cardio phyllus*, *R. arizonicus*, and *R. glaberrimus* in the section *Epirotes* and *R. Collomae*. The new species, *R. Collomae*, is most closely related to *R. alismaefolius* Geyer.

49. RANUNCULUS ALISMAEFOLIUS Geyer. ex Benth. Pl. Hartw. 295. 1848. *R. Bolanderi* Greene, Bull. Calif. Acad. **2**: 58. 1886. *R. Flammula alismifolius* Clements & Clements, Rocky Mt. Flowers 6. 1914, *nomen nudum*.

Glabrous terrestrial or almost palustrine perennials; roots usually 15–30, slender, about 1.5–2 mm. in diameter; stems 3–8 dm. long, mostly 4–6 mm. in diameter, rather freely-branching above, fistulous; radical leaf blades lanceolate, 4–12 cm. long, 1–3 cm. broad, entire or often serrulate, thick, proximally tapering into the petiole and distally blunt; petals 5, obovate, about 10 mm. long, about 5 mm. broad, the nectary scale 1 mm. long, forming a pocket 0.5 mm. deep, the distal half free; achenes 30–50 in a hemispherical to subglobose head 5–7 mm. long and 6–8 mm. in diameter, each achene cuneate-obovate, 2.5 mm. long, 1.7 mm. dorsoventrally, 1 mm. laterally, smooth, glabrous, the margin inconspicuous, the achene beak slender but thick at the base, 0.7–0.9 mm. long, not recurved; receptacle pyriform, 1–2 mm. long in flower and 4–5 mm. long in fruit, glabrous.

Muddy lake borders and ditches at low elevations in the coastal region and up to 1,000 or 1,300 meters inland; Vancouver Island to Eastern British Columbia and Northern Idaho; Lewis County, Falcon Valley, and the eastern border of Washington; Wallowa Mountains, Eastern Oregon, and from the Willamette Valley to the Seaward North Coast Ranges as far south as Mendocino County, California. Northwestern coniferous forest and Palouse grassland. May and June.

[1] Symbols not used previously. *Utah*, Intermountain Herbarium of Utah State College; *MNA*, Museum of Northern Arizona, Flagstaff.

Type collections: (1) *R. alismaefolius,* ". . . Geyerianis e montibus scopulosis. . . " "High grassy plains of Couer d'Aleine. (n. 306), Idaho, cf. Hook. London Jour. Bot. **6**: 66. 1847. (2) *R. Bolanderi,* "Long Valley, Mendocino County California, May, 1886, H. N. Bolander, No. 4730." The TYPE is *HGr. 2409.* (3) *R. flammula alismifolius, nomen nudum,* referred here because of the similarity of the names *alismifolius* and *alismaefolius,* although the authors must have had in mind *R. alismaefolius* var. *montanus,* since it is the only variety occurring in the range covered in the book.

KEY TO THE VARIETIES

Petals 5, obovate.
- Receptacle elongated by 3–5 mm. in fruit, pyriform; stems 3–8 dm. long; leaves lanceolate, often serrulate. ..... 49. *R. alismaefolius.*
- Receptacle elongated by 1 or 2 mm. (rarely more) in fruit; stems 1–4 dm. long; leaves entire.
  - Achenes glabrous; herbage glabrous.
    - Leaves lanceolate; petals about 10 mm. long ..... 49A. Var. *Hartwegii.*
    - Leaves ovate or ovate-lanceolate; petals usually about 6 mm. long ..... 49B. Var. *alismellus.*
  - Achenes pubescent or glabrate; herbage pilose or glabrous; petals 8–16 mm. long; leaves lanceolate ..... 49C. Var. *Lemmonii.*

Petals 10 or rarely 5–9, oblanceolate or sometimes broadly so ..... 49D. Var. *montanus.*

49A. RANUNCULUS ALISMAEFOLIUS var. HARTWEGII (Greene) Jepson, Fl. Calif. **1**: 534. 1922. *R. alismaefolius* var. *caule petiolisque basi hirsutis* Benth. Pl. Hartw. 295. 1848. *R. Hartwegii* Greene, Erythea **3**: 45. 1895. *R. arnoglossus* Greene, Pittonia **4**: 143. 1900.

Glabrous; stems 2–4 dm. long, 1.5–2.5 mm. in diameter, branching above, several-flowered; radical leaf blades lanceolate, 4–10 cm. broad, entire, of intermediate thickness; petals 5, obovate, 6–8 mm. long, the nectary scale attached nearly to the apex, often lobed; achenes 20–30, each 2 mm. long, 1.5 mm. dorsoventrally, 0.8 mm. laterally, the beak about 0.7 mm. long; receptacle 1–1.5 mm. long in fruit.

Mountain meadows at 1,400–2.200 meters elevation; mountains of central Oregon to the Sierra Nevada as far south as Calaveras County, California, and to Southern Idaho; Washoe and Ormsby Counties and the East Humboldt Mountains, Nevada; Helena and Midvale, Montana; Yellowstone National Park and Leckie, Wyoming. Western pine forest. May and June.

Occurring in the Oregon Cascades as an intergrade toward var. *alismellus.*

Type collections: (1) Var. *caule petiolisque basi hirsutis,* "In uliginosus (Bear Valley) montium Sacramento," *Hartweg 1627 (155),* Sierra Nevada in Nevada County, California. (2) *R. Hartwegii.* Based upon the unnamed variety listed above. (3) *R. arnoglossus,* "Subalpine in the Ruby [East Humboldt] Mountains, eastern Nevada; collected by the writer [Greene], 20 July, 1896." The TYPE is *HGr. 2388–9.*

49B. RANUNCULUS ALISMAEFOLIUS var. ALISMELLUS A. Gray, Proc. Am. Acad. **7**: 327. 1868. *R. alismellus* Greene, Fl. Fran. **1**: 297. 1892.

Glabrous; roots 6–12 slender; stems 1–2 or 3 dm. long, 1–1.5 mm. in

diameter, often simple, usually 1- or 2-flowered; radical leaf blades ovate-lanceolate or sometimes ovate, 2–4 cm. long, entire, thin; petals 5, obovate, about 6 mm. long, the nectary scale attached laterally usually almost to the apex, truncate or rounded; achenes 10–30, each 1.5 mm. long, 1.2 mm. dorsoventrally, about 0.5 mm. laterally; receptacle about 1 mm. long in fruit.

Mountain meadows and wet ground near snow banks at 1,400–2,000 meters elevation northward and 2,200–3,300 meters southward; eastern peaks of the Cascade Mountains in central and southern Washington; high mountains of Oregon to the high North Coast Ranges and the San Jacinto Mountains, California; near Virginia City and in the East Humboldt (Ruby) Mountains, Nevada. Mostly northern coniferous forest. June and July.

The Oregon form is more robust and with branching stems, and it is an intermediate toward the variety *Hartwegii*. Typical var. *alismellus* occurs on the eastern side of the Cascade Mountains in Washington.

Type collection: "Lake Tenayo [Tenaya] and on Mt. Dana, Sierra Nevada, to the height of 12,000 feet, Bolander." Yosemite National Park, California. The Lake Tenaya specimen is *Brewer 1684*. Only the Mt. Dana specimen is by Bolander, and it is designated as a LECTOTYPE, *GH*.

49C. RANUNCULUS ALISMAEFOLIUS var. LEMMONII (A. Gray) L. Benson, Am. Jour. Bot. **23**: 172. 1936. *R. Lemmonii* A. Gray, Proc. Am. Acad. **10**: 68. 1875.

Commonly pilose at least on the stems and petioles; stems decumbent, 1.5–3 dm. long, 1.5–3 mm. in diameter; radical leaves lanceolate, 3–9 cm. long, 5–10 mm. broad, entire; petals 5, obovate, 8–16 (mostly 10) mm. long, the nectary scale like the typical species; achenes about 20, each about 2 mm. long, 1.8 mm. dorsoventrally, about 0.8–1 mm. laterally, pubescent, glabrate, or glabrous, the beak 0.5–1 mm. long; receptacle pyriform, 2–5 mm. long in fruit.

Meadows of valleys in the arid mountain region at 1,500–2,000 meters elevation; Modoc County to Truckee, California. Western pine forest. May to July.

Type collection: "Sierra Valley, California, alt. 5,000 feet, J. G. Lemmon." The TYPE is in the Gray Herbarium. The Sierra Valley specimens (apparently isotypes) seen in other herbaria are not this variety. In fact, three or four species are represented among them.

42D. RANUNCULUS ALISMAEFOLIUS var. MONTANUS S. Wats. Rept. U. S. Geol. Expl. 40th. Par. **5**: 7. 1871. *R. calthaeflorus* Greene, Erythea **3**: 45. 1895. *R. alismaefolius* var. *calthaeflorus* Davis, Minn. Bot. Studies **2**: 495. 1900. *R. unguiculatus* Greene, Pittonia **4**: 142. 1900.

Glabrous; stems erect or reclining at the bases, branching above, and the inflorescence cymose but flat-topped, as it is also in *R. alismaefolius* and var. *Hartwegii;* radical leaf blades narrowly elliptic, 2–6 cm. long, 1–2.5 cm. broad, entire, of intermediate thickness, proximally tapering and distally acute; petals 10 (rarely 5–9), 5 or commonly 7–12 mm. long, 2–3 or rarely 5 mm. broad, usually oblanceolate, proportionately much narrower than in

any of the other varieties, the nectary scale forming a broad pocket 0.4–0.5 mm. deep; achenes 25–60, each about 2 mm. long, 1.3 mm. dorsoventrally, 1 mm. laterally; receptacle 2–3 mm. long in fruit.

Mountain meadows at 2,700–3,000 meters; East Humboldt (Ruby) Mountains, Nevada, to Western and Southern Wyoming and Colorado. Northern coniferous and western pine (lodgepole pine) forest. June and July.

Type collections: (1) Var. *montanus,* "Shore of Marian Lake in the East Humboldt [Ruby] Mountains, Nevada, and at the head of the Provo River in the Uintas; 9,000 feet altitude; June–August. (18.)" The collection from the Uintah Mountains by Sereno Watson in 1868 is designated as a LECTOTYPE, GH. In the U. S. National Herbarium the Marian Lake specimen is sheet *No. 862,* and the Uintah plant is mounted on the same sheet (unnumbered). (2) *R. calthaeflorus,* "Plant of the Colorado Rocky Mountains chiefly, at elevations a little below the limit of trees; the *R. alismaefolius,* var. *montanus* of S. Watson, partly; also the type of the unpublished *R. alismaefolius,* of Geyer." At the bottom of the same page, Greene states, "Geyer's specimens, on the labels of which he wrote this [*R. alismaefolius*] as a new name were of the Rocky Mountain species which I now name *R. calthaeflorus.*" Greene confuses Geyer's specimens from the "Rocky Mountains," but actually from Coeur d'Alene, Northern Idaho, with the plants from the southern and central Rocky Mountain System, which is the one he describes as *R. calthaeflorus.* (Note that the petal number is given as 10). That Greene did not know Geyer's plant differed from Watson's variety *montanus* is emphasized further by the following statement, "*R. Hartwegii* of the Californian Sierra differs essentially from the Rocky Mountain *R. calthaeflorus* . . . in its broadly obovate petals only half as numerous, namely five." So also does Geyer's plant (cf. isotype, *S*), which is absolutely identical with Greene's *R. Bolanderi* from coastal California. However, the following is quoted from Greene, "Asa Gray's statement that '*R. Bolanderi,* Greene, Bull. Calif. Acad. ii. 58, answers to the type of this species [*R. alismaefolius*]' is not only without foundation; it proves that the author did not know that Geyer's type was not Californian." What really is proved is that Greene did not understand Geyer's type and knew only that it came from the "Rocky Mountains" and that he was really describing the southern and central Rocky Mountain plant as *R. calthaeflorus,* and not renaming Geyer's species. Several specimens collected prior to 1895 are in the Herbarium Greeneanum and *No. 2391* of that herbarium is designated as a LECTOTYPE of *R. calthaeflorus.* It was collected in wet, boggy ground near Georgetown, Colorado at 12,000 feet altitude by *Chas. S. Sheldon* on August 17, 1884, *No. 281.* (3) *R. unguiculatus,* "Common 'on sites of old snow banks' at 11,500 feet in the mountains of southern Colorado, C. F. Baker, 28 Aug., 1899." The TYPE is *HGr. 2994 and 7801.*

50. RANUNCULUS ORESTERUS L. Benson, apud Benson & Carter, Am. Jour. Bot. **26**: 555. 1939.

Swales at 1,300 meters elevation in the Blue Mountains between Baker and Canyon City, Eastern Oregon; New Meadows, Adams County, Idaho (*Ray J. Davis 94, I S B*), cf. L. Benson, Am. Jour. Bot. **27**: 187–8. 1940. Western pine forest. June.

Type collection: "In swales at the summit of the Blue Mountains, Eastern Oregon, altitude 4,000 feet (fide Washington State College specimen), Baker City-Canyon City road. Known only from the type collection by *William C. Cusick*, June 4, 1902, *No. 2800.* Type specimen in the Dudley Herbarium, Stanford University, California, *No. 96453.* Isotypes: University of Oregon Herbarium, 3 sheets marked by the writer in 1932 with a square containing an x in its lower left corner; Washington State College Herbarium *No. 10201;* New York Botanical Garden." One of the specimens from the University of Oregon was presented to the herbarium of the writer in 1939 through the courtesy of Dr. LeRoy Detling.

51. RANUNCULUS AMBIGENS S. Wats. Bibl. Ind. N. Amer. Bot. **1**: 16. March, 1878 and Proc. Am. Acad. **14**: 289. May 14, 1879. (?) *R. obtusiusculus* Raf. Med. Repos. N. Y. II. **5**: 359. 1808, *nomen dubium*, cf. Fern. Rhodora **38**: 173–5. 1936. *R. Flammula* var. *major* Hook. Fl. Bor. Amer. **1**: 11. 1829. *R. ambigens* var. *obtusiusculus* Davis, Minn. Bot. Studies **2**: 494. 1900, *nomen dubium.*

Wet clay soil at low altitudes; Minnesota to Maine (York) and southward to Louisiana, Tennessee, southeastern Virginia (Appomattox River), and possibly Georgia (Chapman). Mostly coastal in New England. Largely hardwood forests. May to August.

Type collections: (1) *R. obtusiusculus,* "In New-Jersey in marshy places." Observed in 1803 and 1804 by C. Rafinesque-Schmaltz. Fernald, *loc. cit.*, writes as follows, "That Rafinesque's drawing of an *annual,* with bluntish leaves, leafy-bracted peduncles, gamopetalous corolla, linear or linear-lanceolate sepals, and rounded obovate petals (his fig. 2), is not a recognizable illustration of *R. ambigens,* which is a coarse and obvious perennial, with attenuate leaves, bractless peduncles, ovate sepals and distinct (as in all the genus) oblong petals, should be obvious. . . . Except for the alternate leaves the drawing of the habit could as well have been made from a vague recollection of *Lysimachia* (*Steironema*) *lanceolata* as from *Ranunculus ambigens.*" (2) Var. *major,* "Canada. *Mr. Goldie.*" (3) *R. ambigens,* as first published (Bibl. Ind. N. Amer. Bot. **1**: 16. March, 1879) "In inundated places and small rivulets: Pennsylvania & Virginia."

52. RANUNCULUS FLAMMULA L. Sp. Pl. 548. 1753.

Stems reclining, sometimes stoloniferous, rooting adventitiously at the lower nodes, 1–5 dm. long and 2–7 mm. in diameter, branching above and 2–25-flowered, fistulous below, glabrous or with a few stout, appressed hairs; leaves alternate, the blades simple, mostly oblanceolate, or lanceolate or sometimes ovate-lanceolate, 2–6 or 8 cm. long, 3 or 5–10 or 13 mm. broad, entire or serrulate, acute at both ends, glabrous or somewhat appressed-hairy, the petioles mostly 2–7 cm. long; petals 5, 4–8 mm. long, 4–7 mm. broad; stamens 25–50; achenes 20–50 in a globose head 3–5 mm. long and 4–5 mm. in diameter, each achene obovate, 1.4–1.7 mm. long, 1–1.2 mm. dorsoventrally, the achene beak stout, 0.1–0.2 mm. long, straight.

Marshy ground near sea level; Europe; Quiddy Viddy Lake, Newfoundland, and Yarmouth County, Nova Scotia; occurring on the Pacific Slope (Washington and Oregon) as an intergrade to var. *ovalis.* Northern coniferous forest. July to early September.

Type collection: "*Habitat in* Europae *pascuis udis.*"

No one of the three following varieties is wholly clear in its definition. However the populations are well-marked in extreme forms:

52A. RANUNCULUS FLAMMULA var. **ovalis** (Bigel.) L. Benson, comb. nov. *R. filiformis* Michx. var. *ovalis* Bigel. Fl. Bost. Ed. 2. 239. 1824, not *R. ovalis* Raf. in 1814. *R. reptans* L. var. *ovalis* Torr. & Gray, Fl. N. Am. **1**: 16. 1838. *R. unalaschensis* Bess. ex Ledeb. Fl. Ross. **1**: 32. 1842, as syn. *R. Flammula* L. var. *unalaschensis* Ledeb. Bull. Soc. Nat. Mosc. **34**[2]: 41. 1861. *R. reptans* L. var. *strigulosus* Freyn. Deuts. Bot. Monatss. **8**: 181. 1890. *R. microlonchus* Greene, Erythea **4**: 122. 1902. *R. Flammula* var. *varians* Blankinship, Mont. Agric. Coll. Sci. Studies Bot. **1**: 55. 1905. *R. Flammula unalaschensis* Piper, Contr. U. S. Nat. Herb. **11**: 272. 1906. *R. Flammula* L. var. *strigulosus* Freyn ex Peck, Man. Higher Pl. Ore. 302. 1941, nomen nudum.

Stems 1–4.5 dm. long, mostly 0.8–1.5 mm. in diameter, not necessarily rooting at all or any of the nodes; radical leaf blades markedly broader than the petioles, 1–5 cm. long, 1.5–7 or rarely 13 mm. broad, broadest at the middles and tapering to both ends, entire, the petioles 2–6 or up to 13 cm. long; cauline leaves 1–2 or 3 cm. long, 1.5–4 or 6 mm. broad, oblanceolate or broadest at the middles; petals 5, commonly 3.5–5 or rarely 2 or 6.5 mm. long; achene beak 0.3–0.6 mm. long; intermediate in quantitative characters between *R. Flammula* and var. *filiformis*.

Muddy or marshy ground or wet sand from sea level up to 1,000 meters elevation northward or up to 2,500 meters southward; from Alaska southward to north-coastal and montane California, Arizona (Kaibab Forest), and Colorado and eastward to Newfoundland and New England. Summer.

This variety is best-developed in the Western States, especially in the Pacific States. The New England and New York form, to which the type (Boston) must have belonged is really an intermediate between the extreme of var. *ovalis* and var. *filiformis*. For this reason, the name var. *strigulosus* has been previously maintained for the Western form. However, the extreme form occurs here and there in eastern Canada and in the northern tier of states from Minnesota eastward. A form with unusually short, broad, thick radical and cauline leaves occurs in Newfoundland (St. John Bay, *Fernald et al. 28256*, GH; Ingornachoix Bay, *Fernald & Wiegand 3413*, GH.)

Type collections: (1) Var. *ovalis*, "Sent from Danvers by Mr. Nichols." Mr. Weatherby of the Gray Herbarium wrote as follows on January 10, 1939, "We have none of Bigelow's original material of *R. reptans* var. *ovalis*. Whether any exists, I do not know. I have no doubt, however, that the material we have represents this plant." The common, rather broad-leaved form from the vicinity of Boston is accepted as similar to the type. (2) *R. unalaschensis*, "*R. unalaschensis*, Besser in herb. Zeyheri." "Hab. in Unalaschka! (Chamiss., Eschsch.)" This plant was interpreted by Fernald, Rhodora **19**: 137. 1917. as *R. reptans* var. *ovalis*. The type has not been seen. (3) Var. *strigulosus*, "Oregon. Mt. Hood. 24 Juli 1888, leg. Röll." Peck in combining this varietal name under *R. Flammula* gave no reference to Freyn's com-

bination under *R. reptans*. (4) *R. microlonchus*, "Collected by the writer in northern Idaho, August, 1889." Lake Pend Oreille, Greene, Aug. 9, 1889. Type, *HGr 2423*. (5) Var. *varians*, "Crow Creek, Mission Mts. Montana, Aug., 1897, M. J. Elrod, 234." It is possible that the new combination may be published first in Abrams, Ill. Fl. Pac. Sts. vol. 2.

52B. RANUNCULUS FLAMMULA var. FILIFORMIS (Michx.) Hook. *R. reptans* L. Sp. Pl. 549. 1753. *R. filiformis* Michx. Fl. Bor. Am. **1**: 320. 1803. *R. reptans* var. *filiformis* DC. Syst. **1**: 248. 1818. *R. Flammula* var. *intermedia* Hook. Fl. Bor. Am. **1**: 11. 1829, in part. *R. Flammula* var. *filiformis* Hook. Fl. Bor. Am. **1**: 11. 1829. *R. Flammula* var. *reptans* E. Mey. Pl. Lab. 96. 1830. *R. reptans* var. *intermedius* Torr. & Gray, Fl. N. Am. **1**: 16. 1838, in part. *R. intermedius* Heller, Bull. Torrey Club. **25**: 580. 1896, neither Poir. in 1804 nor. Eat. in 1822.

Stems stoloniferous, reclining, rooting adventitiously, 1–3 or rarely 4 dm. long and 0.2–1 mm. in diameter, rarely larger in the lowest internode, branching or unbranched, radical leaves simple, filiform or linear, not or else barely expanded into a blade, 1.5–6 or 9 cm. long, 0.5–1.5 mm. broad, entire, distally truncate with a differentiated (callus or glandular ?) apex, glabrous or with stout, appressed hairs about 2–8 mm. long; cauline leaves in clusters at the nodes where roots enter the soil, actually alternate, the blades expanded, tapering to both ends, 3 mm. long, 1–1.5 or 2 mm. broad, petioled; petals 5 or up to 11, 2–4 or rarely 7 mm. long, 1.3–2.5 or rarely 3.5 mm. broad; stamens 5–25; achenes about 5–15 in a hemispherical cluster 1.5–2.5 mm. long by 2–3.5 mm. in diameter, each achene 1.3–1.6 mm. long, 1.1–1.2 mm. dorsoventrally, the achene beak slender above, 0.3–0.5 or rarely 0.2 or 0.7 mm. long, recurved.

Marshy ground of lakes, streams, and ditches from sea level (northward) to 2,000 meters elevation (southward); Northern Europe and Northern Asia; Alaska to Labrador and Greenland and southward to Bull Lake Creek, Wyoming, and the northern tier of states from Minnesota eastward; New England; Susquehanna River in northeastern Pennsylvania. Northern coniferous and Northeastern hardwood forests. Summer.

Type collections: (1) *R. reptans*, "*Habitat* in Suecia." (2) *R. filiformis*, "HAB. *ad ripas* S. Laurentii et sinum Hudsonis." (3) Var. *intermedia*, "On gravelly banks of rivers from Canada to lat. 60°. *Dr. Richardson. Drummond.* Newfoundland. *Mr. Morrison.*" The description was as follows: "*intermedia;* caule repente gracili, foliis anguste lanceolatis superioribus linearibus integerrimus." According to Fernald, Rhodora **19**: 137. 1917, "It is clear that Hooker was merely separating from the true slender-leaved *R. reptans* (his *R. Flammula filiformis*) a broader-leaved but repent slender plant of Canadian river banks, a plant scarcely separable from *R. reptans*, but somewhat broader-leaved than the typical form of the species."

52C. RANUNCULUS FLAMMULA var. **samolifolius** (Greene) L. Benson, comb. nov. *R. samolifolius* Greene, Pittonia **3**: 13. 1900. *R. reptans* var. *samolifolius* L. Benson, Am. Jour. Bot. **23**: 171. 1936.

Stems 1–4 dm. long, rather stout; leaf blades ovate to obovate or very broadly oblanceolate, 1.5–3 cm. long, 1–1.2 cm. broad, usually sessile and the petioles usually sheathing the stem; otherwise like var. *ovalis*.

Mountain meadows at 1,500–2,000 meters elevation; Cascade Mountains from Klamath County, Oregon to Plumas County, California. Northern Coniferous and Western Pine Forests. Summer.

A fairly well-marked geographical form, the characters of which barely entitle it to varietal rank.

Type collection: "A well-marked species of the higher Sierra Nevada, Calif., from Mt. Shasta southward." The following specimen from the only definite locality mentioned is designated as a LECTOTYPE: Mt. Shasta, *C. H. Dinwiddie* in 1883, *HGr. 2456*. It represents the extreme form of the variety. Publication of this variety in Abram's Illustrated Flora of the Pacific States Vol. 2 may precede publication here.

Significant specimens, cf. L. Benson, Am. Jour. Bot. **23**: 171. 1936.

53. RANUNCULUS HYDROCHAROIDES A. Gray, Mem. Am. Acad. II. **5**: 306. 1855.

Glabrous aquatic or palustrine perennials; stems procumbent or floating or some of them suberect, rooting at the lower nodes, 10–25 cm. long and 1.5–4 mm. in diameter, 1–3-flowered, often fistulous; radical leaf blades simple, ovate, 1.5–3.5 cm. long, 1–2.8 cm. broad, entire, proximally truncate or rarely subcordate and distally usually acute, petioles 2–3.5 cm. long, stipular leaf bases 0.5–1 cm. long; cauline leaves alternate, like the radical, petioled; petals 5.

Marshes, streams, and springs at 2,200 or 2,400 meters; Owens Lake (undoubtedly the Sierra Nevada above it), California; Flagstaff, the White Mountains, and southeastern Arizona; southwestern New Mexico; northwestern Mexico. Western pine forest. June to September.

Type collection: "In wet marshes, Mabibi, Sonora; June." *Thurber.*

53A. RANUNCULUS HYDROCHAROIDES var. STOLONIFER (Hemsl.) L. Benson, Am. Jour. Bot. **27**: 187. 1940. *R. stolonifer* Hemsl. Diagn. Pl. Nov. 17. 1879.

Palustrine; flowering stems erect, 1–3 dm. long, slightly fistulous, stolons 2–4 dm. long; radical leaf blades cordate or ovate, 0.7–3.7 cm. long, 0.4–3 cm. broad, dentate; cauline leaves narrowly elliptic, 1.5–3 cm. long, 0.2–0.8 cm. broad, usually dentate; petals perhaps sometimes more than 5.

Marshy ground of springs and streams in the mountains at about 2,000 meters elevation; Eastern Arizona; New Mexico; Mexico. Western pine forest. Summer.

Type collection: "Mexico, in regione San Luis Potosi, alt. 6000–8000 ped., Perry et Palmer, 4. (Hb. Kew.)"

54. RANUNCULUS GORMANII Greene, Pittonia **3**: 91. 1896. *R. reptans* L. var. *Gormanii* Davis, Minn. Bot. Studies **2**: 498. 1900. *R. terrestris* Wynd, Torreya **30**: 53. 1930.

Boggy mountain meadows at 2,000–2,500 meters; Cascade Mountains from the Three Sisters, Oregon, to the Siskiyou and Klamath Mountains, California. Northern coniferous forest. June and July.

Type collections: (1) *R. Gormanii,* "On moist banks at Cathedral Springs, Crater Lake, in southern Oregon, 22 Aug., 1896, collected by Mr. M. W. Gorman." The TYPE is *HGr. 2408.* (2) *R. terrestris,* "The type has been deposited in the Herbarium of the University of Oregon as:—*Wynd, no. 2086,* Red Blanket Creek in the southwest corner of Crater Lake National Park."

Significant specimens, cf. L. Benson, Am. Jour. Bot. **23**: 172. 1936; Madroño **2**: 129. 1934.

55. RANUNCULUS POPULAGO Greene, Erythea **3**: 19. 1895. *R. Cusickii* Jones, Proc. Calif. Acad. II. **5**: 615. 1895. *R. alismellus* (A. Gray) Greene var. *Populago* Davis, Minn. Bot. Studies **2**: 496. 1900.

Mountain meadows at 1,500–2,000 meters elevation; Blue Mountains, Washington, to the Bitterroot Mountains, Idaho, and the Siskiyou Mountains and Butte County, California. Northern coniferous forest. Summer.

Type collections: (1) *R. Populago,* "A somewhat rare plant of the mountains of eastern Oregon and adjacent Idaho, distributed by Mr. Cusick and others under various names. . . ." Greene, Pittonia **3**: 14. 1896, added the following statement, "RANUNCULUS POPULAGO, Greene, Eryth. iii, 19, has a synonym in *R. Cusickii,* Jones, Proc. Calif. Acad. n. ser. v. 615. Cusick's number 1161 is also my type of the species." The TYPE is *HGr. 2756.* (2) *R. Cusickii,* "The type is No. 1161, Cusick, Eagle Co., Or., 1884, 6000° alt."

Significant specimens, L. Benson Am. Jour. Bot. **23**: 171. 1936; Madroño **2**: 129–130. 1934.

56. RANUNCULUS LAXICAULIS Darby, Bot. S. Sts. 204. 1855. *R. Flammula* L. var. *laxicaulis* Torr. & Gray, Fl. N. Am. **1**: 16. 1838. *R. pusillus* var. *denticulatus* Torr. & Gray, Fl. N. Am. **1**: 17. 1838. *R. texensis* Engelm. apud Engelm. & Gray, Bost. Jour. Nat. Hist. **5**: 210. 1847.

Stems erect or reclining, rooting adventitiously at only the lowest nodes, 1–5 dm. long and 1–5 mm. in diameter, freely branching, fistulous; radical leaf blades simple, oblong to ovate-obtuse, 1–4 cm. long, 6–18 cm. broad, dentate or entire, proximally truncate or rounded and distally truncate or obtuse, petioles 1–7 cm. long, stipular leaf bases 0.5 to about 1 cm. long; petals 5, 3–4 or 7 mm. long, 1.5–2 mm. broad.

Marshy ground and ditches at low elevations; lowlands near the Mississippi River system from Missouri, southern Illinois, and northwestern Kentucky southward to southeastern Texas and thence eastward to northeastern Georgia and northward on the coastal plain to Maryland (Snow Hill) and Delaware (Laurel). River bottom forest. April to June.

Long known as *R. oblongifolius* Ell., which is a synonym for *R. pusillus* Poir.

Type collections: (1) Var. *laxicaulis,* "Milledgeville, Georgia, *Dr. Boykin!*" The writer has not located the Boykin specimen at the New York Botanical Garden or elsewhere. Dr. Fernald, Rhodora **38**: 173–5. 1936, writes as follows concerning applicability of the name *R. laxicaulis* to *R. ambigens* S. Wats. "The Boykin specimen, type of *R. Flammula* β *laxicaulis* is not at the Gray Herbarium and Dr. Gleason writes me that it cannot be

found in the Herbarium of the New York Botanical Garden. Nor have I seen in either herbarium any material [of *R. ambigens*] from the Atlantic States from south of Delaware or Maryland, although there is a specimen without detailed data at New York said on the copied label to be from Georgia. This, however, is one of the many unlocalized sheets from Chapman, too many of which are open to doubt. The petals of *R. ambigens* only slightly exceed the sepals (sepals 5–7 mm. long, petals 5–8 mm. long); but Torrey & Gray described the 'petals . . . three times as long as the calyx.' They also had 'a weak much branched' plant with 'leaves all entire,' not a convincing description of the coarse stem (0.5–2 cm. thick at the base), simple or slightly forking, of *R. ambigens*, which has the middle and upper leaves toothed. Their description suggests *R. oblongifolius* Ell.; at least it is unwise to maintain *R. laxicaulis* for the undoubted *R. ambigens.*" Fernald, Rhodora **41**: 541–2. 1939, argued further as follows: "Both the original Torrey & Gray account of Boykin's plant and the fuller account by Darby are perfect descriptions of the plant erroneously passing as *R. oblongifolius.* This I intimated in 1936 (Rhodora, xxxviii. 175), when I showed that the name *R. laxicaulis* certainly does not belong to *R. ambigens* Wats. Although, as then stated, the type can not be found, the descriptions are so convincing to one who has followed through the surrounding vegetation the 'weak, much branched, declined' stems, 'rooting at the lower joints,' that I now have no hesitation in taking up for *R. oblongifolius* of authors, not Ell. the appropriate name R. LAXICAULIS (T. & G.) Darby." (2) Var. *denticulatus*, "β Texas, *Drummond.*" (3) *R. texensis*, "Margin of ponds, &c. near Houston. April." *F. Lindheimer.* "The collection of 1843 was made on Galveston Island, around Houston, on the Brazos, &c." The specimen at the Gray Herbarium is from Houston, April 1842, legit Lindheimer 1843.

56A. RANUNCULUS LAXICAULIS var. **mississipiensis** (Small) L. Benson, comb. nov. *R. mississipiensis* Small, Bull. Torrey Club **27**: 277. 1900.

Stems 3 or 5–6 mm. in diameter; basal leaves ovate-acute, 3 cm. long, 2 cm. broad, strongly dentate; petals 6–10, 5–9 mm. long, 2–2.5 mm. broad.

Marshy ground at low elevations; Lincoln County (Varner) and Ashley County (Mist.), Arkansas, and "Alluvions of Mississippi." River bottom forest. Early spring.

A rather poorly differentiated variety.

Type collection: "ARKANSAS: Varner, Lincoln Co., April 28, 1898; *Bush*, no. 12. MISSISSIPPI: 'Alluvions.' 1840; *Peck.*" In a conversation with the writer at the New York Botanical Garden about August 1, 1935, Dr. Small designated the Mississippi "alluvions" specimen at the New York Botanical Garden as the TYPE. According to the writer's note, it was collected by Short.

57. RANUNCULUS PUSILLUS Poir. in Lam. Encyc. Meth. **6**: 99. 1804. *R. humilis* Pers. Syn. **2**: 102. 1807. *R. oblongifolius* Ell. Sketch. **2**: 58. 1816. *R. pusillus* var. *muticus* Torr. & Gray, Fl. N. Am. **1**: 17. 1838. *R. pusillus* var. *oblongifolius* Torr. & Gray, Fl. N. Am. **1**: 17. 1838. *R. trachyspermus* Engelm. var. *Lindheimeri* Engelm. apud Engelm. & Gray, Bost. Jour. Nat. Hist. **5**: 211. 1847. *R. pusillus* var. *Lindheimeri* A. Gray, Proc. Am. Acad. **21**: 367. 1886. *R. Biolettii* Greene, Pittonia **2**: 225. 1892.

Radical and lower cauline leaf blades simple, oblong to ovate or rarely cordate, distally truncate or rounded; sepals 1–1.5 mm. long; achenes 15–50 in a hemispherical head about 4 mm. in diameter or an ovoid head 2–4 mm. long by 2–2.5 mm. in diameter, each achene oblong-obovate, 1 mm. long, 0.7 mm. dorsoventrally, 0.3 mm. laterally, smooth or slightly or markedly papillate, glabrous, margin inconspicuous, the style in anthesis 0.1–0.2 mm. long, the achene beak 0.1–0.2 mm. long, receptacle pyriform or spherical, 1.5–2 mm. long in flower and 1.5–3 mm. long in fruit, glabrous.

Shallow water of ditches and marshy ground at low elevations; Missouri to New York, southeastern Texas, and Georgia. April to June.

The form occurring in the Gulf States has strongly-papillate achenes. It has been called var. *Lindheimeri*. This form is either native or naturalized in the seaward Coast Ranges of California from Humboldt County to the Santa Cruz Mountains and eastward to Napa County.

Type collections: (1) *R. pusillus*, "Cette plante croît dans la Caroline, dans les lieux humides & marécageux. Elle m' a été communiquée par M. Bosc, qui l'y a recuellie." (2) *R. humilis*, "*R. pusillus* Poir. enc. bot. 6. p. 99. *R. Flammula* Walter. Hab. in Carol. humilis." (3) *R. oblongifolius*, "Collected 12 miles from Savannah on the Augusta road. St. John's Berkley. Dr. Macbride." According to Fernald, Rhodora **41**: 542. 1939, ". . . When Mr. Long and I studied Elliott's material at Charleston in early April, . . . we found that the type of *R. oblongifolius* is characteristic large material of *R. pusillus*. . . ." (4) Var. *muticus*, "New York! to Pennsylvania." The specimen in the New York Botanical Garden, labelled Torrey, Flora of New York (abbreviated) is designated as a LECTOTYPE. (5) Var. *Lindheimeri*, "Near Houston, etc. but not growing together with No. 2 [*R. trachyspermus*]," *Lindheimer* in 1843. (6) *R. Bioletti*, "On Hood's Peak, Sonoma Co., California, May 1, 1889, Mr. F. T. Bioletti."

57A. RANUNCULUS PUSILLUS var. **angustifolius** (Engelm.) L. Benson, comb. nov. *R. trachyspermus* Engelm. apud Engelm. & Gray, Bost. Jour. Nat. Hist. **5**: 211. 1847, not Ell. in 1816. *R. trachyspermus* var. *angustifolius* Engelm. apud Engelm. & Gray, Bost. Jour. Nat. Hist. **5**: 211. 1847. *R. tener* Mohr, Contr. U. S. Nat. Herb. **6**: 513. 1901.

Lower leaves commonly distally acute; sepals 1.5–2 mm. long; achenes 50–125, rarely fewer, in a cylindrical head usually 5–8 mm. long, each achene densely and conspicuously papillate; receptacle cylindrical, 4–7 mm. long in fruit.

Ditches and marshy ground; southeastern Texas; Auburn and Mobile, Alabama. River bottom forest. April to June.

Type collections: (1) *R. trachyspermus*, "Margin of ponds near Huston, &c.," *Lindheimer*. The specimen in the Gray Herbarium bearing Engelmann's label was collected in April 1842, *legit* Lindheimer in 1843; Houston, Texas. It is numbered 2. (2) Var. *angustifolius*, "Near Houston, etc. but not growing together with No. 2 [*R. trachyspermus*]," *Lindheimer* in 1843. The specimen is number 3. (3) *R. tener*. *Nomen novum* for *R. trachyspermus*.

58. RANUNCULUS ALVEOLATUS Carter, apud Benson & Carter, Am. Jour. Bot. **26**: 555. 1939.

Margins of ponds and marshy areas along small streams up to 1,000 meters elevation; Sierra Nevada foothills from Calaveras County to Placer County, California. Oak woodland. April and May.

Type collection: "The type specimen was collected between Fair Oaks and Folsom, 1½ miles southeast of Orangevale. Sacramento County, April 25, 1937, *Annetta Carter 1244* (*Herbarium of the University of California No. 604080.*)"

SECT. 5. HECATONIA (LOUR.) DC.

Styles and achene beaks practically lacking, the stigmas nearly sessile; achene with or without corky thickening of the pericarp.
Achenes smooth on the faces; receptacle not more than 5 mm. long in fruit; perennials; stems rooting at the nodes.
Leaves not cordate at the bases; achenes 10–20; receptacle but slightly enlarged in fruit, 1.5 mm. long ..... 58. *R. hyperboreus*
Leaves (at least some of them) cordate at the bases; achenes 20–60; receptacle greatly enlarged in fruit, 3–5 mm. long ..... 59. *R. natans*
Achenes marked on each face by either minute rough transverse ridges or by a circle of "pin pricks" at the inner margin of the peripheral pericarp thickening; annuals; stems never rooting adventitiously except in one rare variety; receptacle greatly enlarged in fruit, 2.5–9 mm. long ..... 60. *R. sceleratus.*
Styles and achene beaks well-developed, the beaks at least half as long as the achene bodies, 0.6–1.5 mm. long; achenes with conspicuous corky thickening of either the keel or the pericarp beside the keel.
Achenes each with corky thickening beside the inconspicuous keel (especially in the basal and ventral regions); leaves once- or twice-parted or -lobed, pentagonal, 1–2 cm. long by 1.5–2.5 cm. broad; anthers elliptic, 0.5–1 mm. long; petals 4–7 mm. long ..... 61. *R. Gmelinii.*
Achenes each with a conspicuous corky keel; leaves of aquatic specimens finely dissected into ribbon-like segments 1–2 mm. broad, the blades 1.5–10 cm. long and 2–12 cm. broad; anthers oblong, 1–1.5 mm. long; petals 7–15 mm. long ..... 62. *R. flabellaris*

58. RANUNCULUS HYPERBOREUS Rottb. Skrift. Kjoeb. Selsk. **10**: 458. 1770. *R. hyperboreus* f. *fluitans Porsild*, Meddel. Groenl. **50**: 375. 1912.

Marshy ground in boreal regions near the sea; circumboreal; from Alaska along the shore and islands of the Arctic Ocean to Greenland; Old Hollowtop, near Pony, Montana. Arctic-Alpine Grassland. July to August.

Type collection: (1) *R. hyperboreus*, "Island." The title of the Article is "Rare Planter som i Island of Grønland." (2) F. *fluitans*, "Neighborhood of Prøven 7 the northern district of Umanaq . . . occurs in pools."

59. RANUNCULUS NATANS C. A. Mey. in Ledeb. Ic. **2**: 114. 1830. *R. hyperboreus* Wahl. var. *natans* Regel, Reisen Ost-Sib. **1**: 43. 1861. *R. intertextus* Greene, Ottawa Nat. **16**: 33. 1902.

Ponds and lakes at 2,000–2,700 meters elevation in the Central Rocky Mountains and at lower elevations northward; Siberia; Nordegg, Alberta;

Custer County and Beaver Canyon, Idaho; Wyoming and Colorado. Northern Coniferous Forest. July and August.

Type collections: (1) *R. natans*, "Hab. in aquis stagnatibus ad fl. Tscharysch, in fl. Mön et Tegagon in fl. Tschiya influentibus." Flora Rossicam-Altaicam. (2) *R. intertextus*, "Common almost throughout the Rocky Mountains, as an aquatic of subalpine ponds and swamps." "Hitherto referred to *R. natans* of Europe."

60. RANUNCULUS SCELERATUS L. Sp. Pl. 551. 1753.

Stems erect, never rooting adventitiously, 1–10 dm. long and 2–15 mm. in diameter; radical leaf blades simple, reniform, 1–3 or 6 cm. long, 1.5–5 or 10 cm. broad, deeply 3-parted or -divided, the primary parts or divisions usually merely lobed, but sometimes parted or divided, the ultimate lobes obtuse, the sinuses rounded, proximally cordate and distally rounded, petioles 3–12 cm. long, stipular leaf bases 5–10 mm. long, broad; each achene obovate, 0.8–1 mm. long, 0.6 mm. dorsoventrally, 0.3 mm. laterally, with minute, irregular transverse ridges in the central unthickened portion of each face, the periphery of the pericarp at least somewhat corky-thickened, glabrous, marginal keel obscure, the style and the achene beak almost lacking, 0.1 mm. long, not recurved.

Borders of lakes and marsh-land at low elevations; Europe; naturalized about Seattle and the islands of Puget Sound, Washington, and at Portland, Oregon; native or naturalized from Michigan and Missouri to Rivere du Loup, Quebec, and York Harbor, Maine, and southward to North Carolina and the Louisiana Delta Region. Mostly coastal in New England. Hardwood, river bottom, and southeastern pine forests. June to September.

Type collection: "Habitat ad Europae fossas & paludes."

60A. RANUNCULUS SCELERATUS var. MULTIFIDUS Nutt. in Torr. & Gray, Fl. N. Am. **1**: 19. 1838. *R. eremogenes* Greene, Erythea **4**: 121. 1896. *R. eremogenes* var. *degener* Greene, Pittonia **4**: 144. 1900. *R. eremogenes* var. *pilosulus* Greene, Pl. Baker, **3**: 2. 1901. *R. eremogenes* var. *pubescens* Lunell. Bull. Leeds Harb. (2): 6. 1908. *R. sceleratus* var. *eremogenes* Garrett, Spring Fl. Wasatch Reg. 25. 1911.

Radical leaves usually with the primary parts or divisions again deeply parted or divided; pericarp smooth except for a circle of minute "pin prick" depressions on each face at the inner margin of the peripheral thickened zone; otherwise like the typical species.

Borders of lakes, ponds, and streams at 1,000–2,100 meters elevation; Alaska (Matanuska) and the Yukon to the Great Basin and the Great Plains as far south as California (northeastern Siskiyou County and Modoc County), Nevada, and Colorado; Sacaton, Arizona, and Rio Arriba and Grant Counties, New Mexico; Minnesota. Best-developed in the northern desert and the plains grassland. May to August.

Type collections: (1) Var. *multifidus*, "Ponds of the Platte, Nuttall." (2) *R. eremogenes*, "Plant of wet springy places and margins of pools in the West American desert regions, through the Great Basin, and to southeastern Oregon and northwestern British America; the American counter-

part of the Old World *R. sceleratus*, to which it has been erroneously referred, being the *R. sceleratus*, var. *multifidus* of Nuttall. . . . Though first detected by Nuttall on the plains of the Platte, the most luxuriant specimens seen by me are from the region of the muddy lakes that lie along the northwestern border of the Great Basin in northeastern California and adjacent Oregon. Smaller specimens, with leaves more finely divided were collected beyond the British boundary, on Milk River Ridge, by Mr. Macoun, in 1895 (n. 10036). . . ." Apparently *R. eremogenes* was intended as a nomen novum for *R. sceleratus* var. *multifidus*, and that is the interpretation of the writer. Therefore, Nuttall's collection from "Ponds of the Platte" is considered to be the TYPE of this species. (3) Var. *degener*, "Obtained in southern Colorado, in the summer of 1899, by C. F. Baker, perhaps near Pagosa Springs, but the label has been lost." *HGr. 2929* and *2930* have C. F. Baker's Pagosa Springs labels and these two sheets are designated as a LECTOTYPE. (4) Var. *pilosulus*, "In damp places above Gunnison, 17 July, n. 454." *C. F. Baker.* The type specimen in the Herbarium Greeneanum is not numbered with the stamp used on the other sheets. The following is quoted from the label, "in damp spots in bottoms." (5) Var. *pubescens*, Leeds, *Lunell.*

60B. RANUNCULUS SCELERATUS var. **longissimus** (Lunell) L. Benson, comb. nov. *R. eremogenes* Greene var. *longissimus* Lunell, Am. Midl. Nat. **1**: 206. 1910.

Glabrous aquatic; stem of the type specimen exceeding 7 dm. above the point of breaking (when collected); leaves all cauline, 1.8–2.3 cm. long, 3–4.3 cm. long, 3-parted, the parts broadly cuneate, again 3–7-lobed or -cleft, the lobes rounded; petioles from submersed nodes up to 35 cm. long, the *stem producing long filiform adventitious roots;* mature fruit unknown.

Running water, Leeds, North Dakota. Summer.

Type collection: "In running water Leeds [North Dakota], June 27, 1909. Plant rooting from the nodes with long, slender fibers, the lower leaves very long-petioled." (Quoted from the label of the TYPE specimen, *Herbarium of the University of Minnesota 257628.*) Collected by *Lunell.*

61. RANUNCULUS GMELINII DC. var. **terrestris** (Ledeb.) L. Benson, comb. nov. *R. Purshii* Richards, Bot. App. Frankl. 1st. Jour. 751. 1823. *R. fistulosus* Pursh ex Torr. Ann. Lyc. N. Y. **2**: 163. 1826, as syn. *R. limosus* Nutt. in Torr. & Gray, Fl. N. Am. **1**: 20. 1838. *R. Purshii* var. *terrestris Ledeb. Fl. Ross.* **1**: 35. 1842. *R. multifidus* Pursh var. *repens* S. Wats. Rept. U. S. Geol. Expl. 40th. Par. **5**: 8. 1871. *R. Purshii* var. *dissectus* Lunell, Bull. Leeds Herb. (2): 6. 1908. *R. Purshii* var. *geranioides* Lunell, Bull. Leeds Herb. (2): 6. 1908. *R. Purshii* var. *radicans* Lunell, Bull. Leeds Herb. (2): 6. 1908. *R. Gmelinii* var. *Purshii* Hara, Rhodora **41**: 386. 1939. *R. Gmelinii* var. *limosus* Hara, Rhodora **41**: 386. 1939.

Glabrous or hairy palustrine or aquatic perennials; stems reclining or floating, rooting adventitiously, 1–4 dm. long and 1.5–3 mm. in diameter, a little branched, commonly 1–4-flowered, fistulous; leaves all cauline and alternate or the basal present and longer-petioled, the blades compactly pentagonal, 1–2 cm. long, 1.5–2.5 cm. broad, very rarely larger, deeply 3-parted or -divided, the divisions 2–3 times forked or sometimes dissected

into ribbon-like divisions, proximally deeply cordate and distally rounded, petioles 1–3 or 4 cm. long, stipular leaf bases 3–6 cm. long; bracts 1–3; petals 5, yellow, circular or obovate, 4–7 mm. long, 3–6 mm. broad, the nectary scale glabrous, its margins prolonged into flaps, the tips of which are usually free from the petal, or the margins joined distally or sometimes as in *R. flabellaris*.

Mud or sometimes shallow water of lakes, stream borders, and marshes up to 1,500 or 2,000 meters elevation; Alaska to 58° 50′ N. Lat. in Keewatin, and to Prince Edward Island and Nova Scotia and southward to Oregon (Klamath Lake), Nevada (Humboldt Wells), Colorado, North Dakota, Minnesota, Michigan, and Maine (Aroostook County); one collection from New Mexico. Northern coniferous, western pine, and northeastern pine forests; plains and prairie grassland. Late May to August.

Type collections: (1) *R. Purshii*, "(W. B.)" "(W) Denotes the wooded country from lat. 54° to 64° north." "(B) Denotes the Barren Grounds from Point Lake to the Arctic Sea." Collected by Richardson. (2) *R. limosus*, "Margins of ponds in the eastern ranges of the Rocky Mountains, Lewis's River, &c. . . . Nutt." (3) var. *terrestris*, "Hab. ad sin: Eschscholtzii in plaga artica Americae boreali-occidentalis! (Chamiss., Eschscholtz, Hook. et Arn.)" (4) Var. *repens*, "Weber Valley, Utah; altitude 5,000 feet; August." *S.* Watson. (5) Var. *dissectus*, "The lobes just as deeply cut [as in var. *schizanthus*], but the segments broader (as in Geranium dissectum L.) The prevalent land form." The specimen collected by Lunell "In margine paludis" at Leeds, Benson County, North Dakota, June 18, 1906 is designated as a LECTOTYPE, *UM 257716*. (6) Var. *geranioides*, "The lobes not as deeply cleft, and the segments still broader than in var. dissectus (the leaf resembles in outline Geranium molle L.)" The specimen collected at Leeds, North Dakota, June 16, 1900, *Lunell 445* is designated as a LECTOTYPE, *UM 257708*. (7) Var. *radicans*, "Creeping, and rooting repeatedly from the nodes. Leaves mostly the form of var. **geranioides.**" The specimen collected in mud on the peninsula of Lake Ibsen, Benson County, North Dakota, July 6, 1908 by Lunell is designated as a LECTOTYPE, *UM 299854*. *R. Purshii* var. *humifusus* Lunell, Amer. Midl. Nat. **4**: 358. 1916, is a new name for *R. radicans* Regel, Reisen in den Suden von Ost-Sibirien or Pl. Radd. **1**: 44–5. 1861. It is based upon an Old World type, as follows: "Am nördlichen Ufer des Baikel auf sumpsigen Wiesen."

61A. RANUNCULUS GMELINII var. **yukonensis** (Britt.) L. Benson, comb. nov. *R. yukonensis* Britt. Bull. N. Y. Bot. Gard. **2**: 169. 1901. *R. Purshii* subsp. *yukonensis* Porsild, Rhodora **41**: 229. 1939.

Palustrine; stems 0.5–2 dm. long; leaves about 0.8–1 cm. in diameter.

Northern Alaska (reported) and the Yukon District; Marble Mountains, British Columbia (Upper Hat Creek, 3,000 feet, *J. W.* & *Emily M. Thompson 356, T, B,* July 12, 1938). Northern coniferous forest. Summer.

Type collection: "Mouth of the Bonanza Creek, Dawson, June 18, 1899, R. S. Williams (type)."

61B RANUNCULUS GMELINII var. PROLIFICUS (Fern.) Hara, Rhodora **41**: 386. 1939. *R. multifidus* Pursh. var. *terrestris* A. Gray, Man. Ed. **5**: 41.

1867, not *R. Purshii* var. *terrestris* Ledeb. in 1842 (*R. Gmelinii* var. *terrestris* L. Benson). *R. limoso* × *sceleratus* Greene, Pittonia **2**: 65. 1890. *R. lacustris* Beck & Tracy var. *terrestris* McMillan, Metasp. Minn. Valley 247. 1892. *R. delphinifolius* Torr. var. *terrestris* Farwell, Ann. Rept. Comm. Parks & Boulev. Detroit **11**: 63. 1900. *R. delphinifolius terrestris* Piper, Contr. U. S. Nat. Herb. **11**: 272. 1906. *R. delphinifolius* f. *terrestris* Blake, Rhodora **15**: 164. 1913. *R. Purshii* var. *prolificus* Fern. Rhodora **19**: 135. 1917.

Stems upright; flowers paniculate, about 7–50 per stem; bracts numerous; otherwise like the first variety.

Muddy ground of stream and lake banks at low elevations; in scattered northern localities; Montpelier, Idaho; Belgrade and Bozeman, Montana; Michigan; Magdalen Islands, Quebec. Northern coniferous forest. Summer.

Type collections: (1) Var. terrestris, "Ann Arbor, Michigan, on muddy banks, Miss Clark." Cf. Fern Rhodora **38**: 173. 1936. (2) *R. limoso* × *sceleratus*, "I obtained it in July last, on the muddy shores of Bear Lake, near Montpelier, Idaho." *Greene* in 1889. The TYPE is *HGr. 1171.* (3) Var. *prolificus*, "MAGDALEN ISLANDS: Wet meadow, Grindstone, July 22, 1912, *Fernald, Bartram, Long, & St. John*, no. 7482. (TYPE in Gray Herb.)"

61C. RANUNCULUS GMELINII var. **schizanthus** (Lunell) L. Benson, comb. nov. *R. Purshii* var. *schizanthus* Lunell, Bull. Leeds Herb. (2): 6. 1908. *R. Purshii* var. *polymorphus* Lunell, Bull. Leeds Herb. (2): 6. 1908.

Leaves all more or less deeply dissected, the aerial ones deeply 3-parted or -divided and again 2–3 times parted and cleft, about 3–3.5 cm. in diameter, the submersed ones finely dissected into linear ribbons 1–2 mm. broad, the blades 6–9 cm. in diameter; petals obdeltoid, 6–7 mm. long, 6–7 mm. broad, 2–3-lobed or -cleft, the nectary scales as in *R. flabellaris.*

Sloughs and lake borders at Leeds and Lake Ibsen, Benson County, North Dakota. Known only from the collections of Dr. J. Lunell. Prairie grassland. May and June.

It is possible that this is really a form of *R. flabellaris.* The fruit is unknown.

Type collections: (1) Var. *schizanthus*, "Leaves divided into three lobes, and the lobes finely dissected." No type collection given. The specimen in the Herbarium of the University of Minnesota, collected along sloughs at Leeds, North Dakota, June 1, 1903, *Lunell 448* is designated as a LECTOTYPE, *UM 257701* and *257702.* (2) Var. *polymorphus*, "The emersed leaves present forms 1, 2, and 3 just described. The submersed leaves are capillary multifid (filiform dissected). Stems elongated, sometimes several meters in length." No type collection given. The collection from the Peninsula of Lake Ibsen, North Dakota, May 23, 1908, *Lunell 447* is designated as a LECTOTYPE. It is *UM 257709*, *257710*, and *257711.* The epithet *schizanthus* was applied to a palustrine form and the epithet *polymorphus* to an aquatic form.

62. RANUNCULUS FLABELLARIS Raf. apud Bigel, Amer. Mo. Mag. **3**: 344. March, 1818. *R. multifidus* Pursh, Fl. Amer. Sept. **2**: 736. 1814, not Forsk. in 1775. *R. fluviatilis* Bigel. Fl. Bost. Ed. 1. 139. 1814, not Willd. in 1799.

R. delphinifolius Torr. in A. Eat. Man. Bot. Ed. 2. 395. May or later, 1818, cf. Fern. Rhodora **38**: 171–3. 1936. *R. lacustris* Beck & Tracy in A. Eat. Man. Bot. Ed. 3. 423. 1822. *R. missouriensis* Greene, Erythea **3**: 20. 1895. *R. delphinifolius* f. *submersus* Gluck, Beih. Bot. Cent. **39** (2): 328. 1923. *R. flabellaris* f. *riparius* Fern. Rhodora **38**: 171. 1936.

Shallow water or mud up to 1,500 meters elevation in the West; British Columbia to Eastern Washington and Oregon, the lower Columbia River, to Humboldt, Mendocino, and Modoc Counties, California, to Star Valley, Nevada; and east to Ontario, Maine, and New Jersey; south in the Mississippi Valley to Louisiana. Western pine forest; plains and prairie grassland; harwood forests.

Type collections: (1) *R. multifidus*, "In Upper Louisiana . . . *Bradbury* . . . *v. s. in herb. Bradbury.*" (2) *R. fluviatilis*, "In a pond on Brighton road and elsewhere in deep water." "Within 5 or 10 mi. of Boston." 1812–3. *Bigelow.* (3) *R. flabellaris.* Nomen novum for *R. fluviatilis* Bigel. (4) *R. delphinifolius*, none given. Northern and Middle States. (5) *R. lacustris*, "Very abundant in a small lake east of the village of Lansingburgh," Hudson River, cf. N. Y. Med. & Phys. Jour. **2**: 112. 1823. (6) *R. missouriensis*, "A Missouri species, distributed by Mr. Bush." Apparently the type of this species was not noted by the writer at the Hebaruim Greeneanum in the summer of 1935. (7) *F. submersus*, grown from seed "von Bingen im Staate Washington." (8) *F. terrestris*, grown from seed "von Bingen im Staate Washington." (9) *F. riparius*, Nomen novum for f. *terrestris* above.

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MASS COLLECTIONS: DIERVILLA LONICERA

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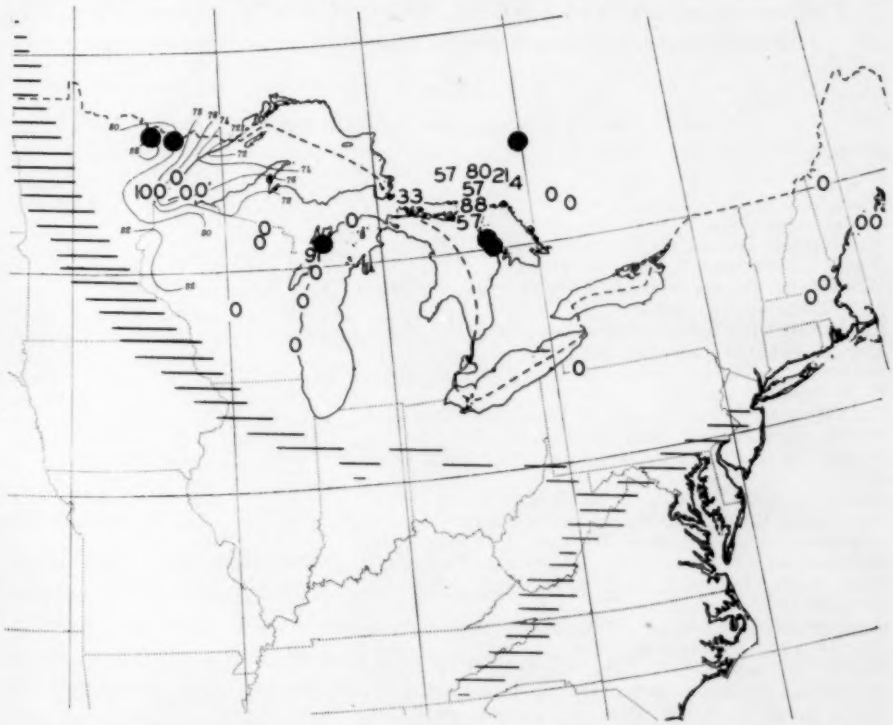
In the summers of 1940 and 1941 mass collections were made of *Diervilla Lonicera*, from Minnesota to Maine. Each collection consisted of a twig with one or more pairs of leaves and with flowers or fruits if they were present; these specimens were collected far enough apart to avoid the taking of more than one from a clone. Many of these collections were made possible by a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Examinations of mass collections, totalling some 673 individuals, corroborates in every detail the words of Professor Fernald accompanying his description of var. *hypomalaca*,[1] as follows: "Typical wide-ranging *Diervilla Lonicera* has the leaves glabrous or at most a little setulose along the midrib beneath. Var. *hypomalaca*, known only from a limited area in the range, is striking on account of the dense white pilosity of the lower surfaces of the leaves." There are further details concerning these plants which cannot be studied from conventional herbarium specimens, but upon which light is shed by mass collections.

Pubescence on different parts of the plant acts in various ways. The calyx-lobes and leaf-margins are ciliate, and the ciliation appears to be uni-

TABLE 1

Number of each leaf-type in mass collections of D. Lonicera

	Typical	Intermediate	Var. *hypomalaca*
MINNESOTA: Duluth, Sept. 5, 1940, no. 21417[a]	0	0	10
Two Harbors, Sept. 5, 1940, no. 21257	22	0	0
WISCONSIN: Ravine west of Herbster, Aug. 26, 1940, *L. H. Shinners*, no. 3449	31	0	0
Road to Redcliff Indian Reservation, Bayfield County, Aug. 25, 1940, *Shinners*, no. 3450	11	0	0
Sandy loam, Found Lake, Saynor, June 27, 1941, *F. W. Stearns*, no. 763	39	0	0
Outwash soil, Stormy Camp, on Wisconsin River east of Woodruff, June 27, 1941, *Stearns*, no. 777	10	0	0
Saddle Mound, south of Pray, Aug. 23, 1940, *Shinners*, no. 2713	16	0	0
Shore of Lake Michigan, Peninsula State Park, Fish Creek, Sept. 28, 1940, no. 21258	2	1	19
Limestone beach, Baileys Harbor, July 13, 1940, *Shinners*, no. 2196	35	0	0
Sand dunes, Whitefish Bay, Door County, July 22, 1940, *Shinners*, no. 3447	15	0	0
Sand dunes, Point Beach State Forest, Two Rivers, July 19, 1940, *Shinners* no. 2448	10	0	0
Top of ravine, Doctors Park, north of Fox Point, Milwaukee, Sept. 22, 1940, *Shinners*, no. 3444.	10	0	0
Bluffs north of Klode Park, Milwaukee, Sept. 22, 1940, *Shinners*, no. 3445	2	0	0
Milwaukee River bank north of Locust St., Milwaukee, Sept. 17, 1940, *Shinners*, no. 3446	3	0	0
MICHIGAN: Wooded dunes, Manistique, July 12, 1941, no. 21259	3	0	0
Wooded dunes, Point Seul Choix, July 12, 1941, no. 21260	8	0	0
ONTARIO: Moist woods at foot of bluff, Garden River, July 13, 1941, no. 21261	12	2	4

[a] When a number is given without collector's name the writer was the collector.

[1] Rhodora 42: 144. 1940.

TABLE 1 (*Continued*)

Number of each leaf-type in mass collections of D. Lonicera

	Typical	Intermediate	Var. *hypomalaca*
Along road on rocks, woods, etc., from Little Current to West Bay, Manitoulin Island, July 14, 1941, no. 21262	20	2	24
Pine woods, etc., Great Cloche Island, 2 miles north of Little Current, July 14, 1941, no. 21263	3	0	22
Woods and roadside, 3 miles north of Willisville, July 13, 1941, no. 21264	9	0	12
Granite knob south of Espanola, July 14, 1941, no. 21265	12	3	13
Granite knob east of McKerrow, July 14, 1941, no. 21266	4	2	14
Granite knob at Simon Lake Park, 6 miles west of Copper Cliff, July 14, 1941, no. 21267	19	0	5
Granite knob east of Sudbury, July 15, 1941, no. 21268	27	0	1
Granite knob between North Bay and Callender, July 15, 1941, no. 21269	36	0	0
Hillside and ledges 19 miles east of Mattawa, July 15, 1941, no. 21270	27	0	0
Woods and roadside, Rockland, July 16, 1941, no. 21271	3	0	0
NEW YORK: Wooded roadside, Jones Mt., Steamburg, June 22, 1940, no. 21272	60	0	0
MASSACHUSETTS: Exposed rocks at summit of Mt. Wachusett, Princeton, Aug. 1, 1941, no. 21273	21	0	0
NEW HAMPSHIRE: Rocky roadsides, Londonderry, Aug. 3, 1941, no. 21274	9	0	0
MAINE: Dallas Plantation, north of Rangeley, July 24, 1940, no. 21275	9	0	0
Woods, Southport, July 24, 1941, no. 21276	20	0	0
Exposed ledges, east side of Monhegan Island, Aug. 22, 1941, no. 21277	31	0	0
Totals:	539	10	114

form throughout the species. On some leaves the midribs (and veins) are setulose below, as is mentioned in Professor Fernald's paper. The number of plants showing this character varies irregularly in mass collections, and close inspection of a number of herbarium specimens shows that some leaves on a plant may be completely glabrous and others on the same plant have setulose midribs.

In table 1 the collections are listed, with the number of individuals of each type represented. From the figures in this table have been computed the percentages of var. *hypomalaca* at each station (including as the variety the intermediates and plants with appressed hairs on the leaves), and these percentages have been placed on figure 1. The variety appears in three areas: one is from Bruce Peninsula, Ontario, northward, a second is in Door County, Wisconsin, and a third is in northeastern Minnesota. It is quite possible that further collections from the Upper Peninsula of Michigan and

from the country north of Lake Superior would show these three areas actually to be confluent. With our present limited data, however, we must for the present discuss these as three separate areas.

In Ontario, from Great Cloche Island (88 per cent on figure 1) to McKerrow (80 per cent), appears a center where each colony of *Diervilla Lonicera* consists of a large majority of var. *hypomalaca;* to the east and west, and possibly to the south (data are lacking to the north), the percentages of velvety-leaved plants in each colony drops progressively. To the east, in particular, is exhibited a well-marked cline.[2]

In Door County, Wisconsin, var. *hypomalaca* appears in but one mass collection, where it makes up 91 per cent, comprising 20 individuals of 22. That these 20 individuals do not represent merely one extensive clone is shown by slight individual variations in nature and density of pilosity and in color of leaves. This collection is from a limestone beach on the Green Bay side of the peninsula, which is the region of origin of one of the original sheets cited with the description of the variety, and of the only sheet in the Herbarium of the University of Wisconsin. Two other mass collections from Door County, comprising 50 individuals, include none of the variety. These two collections are from the Lake Michigan side of the peninsula; one is on sand, and the other on a limestone beach. Soils differences are not, then, responsible for the differences between the two sides of the peninsula. Var. *hypomalaca* occurs only in the northern part of the range of *D. Lonicera*, but the west side of Door County, where it is found, is warmer and less humid[3] than the east side, where it has not been found.

In Minnesota, as in the region just discussed, the occurrence of var. *hypomalaca* does not appear to be related to low temperature. A mass collecleection from the heights above Duluth is made up entirely of the variety, and from there it occurs northward; two herbarium specimens have been taken near the Canadian border.[4] The region north of Duluth is warmer than the Lake Superior shore, as is shown by the July average maximum isotherms on figure 1.[5] The boreal plants of this region ordinarily occur, not northward from Duluth, but northeastward along the Lake Superior shore, but the velvety-leaved variety is absent from the one mass collection from Two Harbors and is not represented by herbarium specimens.

Pilosity of lower leaf-surface in *Diervilla Lonicera* is definitely not a response to exposure. The three collections from Lake Huron northward (57

[2] A cline is "a chain or gradient of differences arranged in a definite direction." Goldschmidt, R. B., *The Material Basis of Evolution*, p. 65.

[3] Cf. Fassett, Ann. Mo. Bot. Gard **28**: 337–338. 1941.

[4] Loaned from the Herbarium of the University of Minnesota by Professor C. O. Rosendahl.

[5] Data from *Climatic summary of the United States*, Section 44—Northern Minnesota, p. 18.

per cent, 88 per cent, and 57 per cent, respectively, on figure 1) were each made partly in the open and partly in the woods, and it was observed in the field that there was no correlation of exposure and pilosity. From near Espanola to Callender, Ontario, all collections were made in the same habitat, namely the heavily glaciated, almost bare, granite knobs, and these collections show a well-marked cline (80 per cent, 21 per cent, 4 per cent, 0 per cent). That the percentage of occurrence of the variety is not affected by exposure is further indicated by the collections from the heavily glaciated summit of Mt. Wachusett, Massachusetts, and from the sea-cliffs of Monhegan Island, Maine; both are similar to the granite knobs of Ontario but neither has any pilose plants. Var. *hypomalaca* is strictly limited to a geographic area without respect to any observed ecological factor.

The varieties of *D. Lonicera* cross a conspicuous lithological boundary. Manitoulin Island (57 per cent on figure 1) and Great Cloche Island (88 per cent on figure 1) are composed of Silurian and Ordovician limestones, but a few miles north of Great Cloche Island there is an abrupt change, the limestone giving way to granites, quartzites, etc., of Huronian and Pre-Huronian age. Neither the abundance of the plant nor the percentages of its varieties seem to be affected by this change in rock type.

The distribution of *D. Lonicera* var. *hypomalaca*, not being related in any obvious way to ecological factors, must be the result of its history. Perhaps it represents a mutation which has infiltrated the species from a single center of origin; perhaps it is a pubescent race, once occupying a region north of the Great Lakes, which has been submerged by the spread of the glabrous race.

Goldschmidt[6] writes, "One of the most remarkable features of these clines of subspecific characters is that they frequently occur in the form of a continuous fluctuation of characters, so that two distinct forms are connected by a continuous series of intermediate conditions." Such gradations between varieties and the typical forms of their species may be readily recalled, but such is not the case here. Of 673 individuals, including 134 of var. *hypomalaca*, but 10 have pubescence so sparse or inconspicuous that they may be considered intermediate, and these are all in collections where well-developed individuals of the variety are in the majority. The gradation consists less of the development of intermediate individuals than in the varying numbers, at each locality, of definitely pilose individuals as compared to the number of definitely glabrous individuals.

A few plants from the Manitoulin Island collection, where 57 per cent of the individuals are var. *hypomalaca*, have the lower leaf-surfaces without the ordinary velvety pilosity of the variety, but rather with copious long straight appressed hairs. These plants are treated as var. *hypomalaca*.

[6] L.c., p. 66.

A strange individual was collected in the woods a few miles south of Mt. Wachusett, Massachusetts. Two stems arise from opposite sides of the root-stock; one is normal and the other has alternate leaves.

SUGGESTIONS

Solution to these problems in taxonomy and phytogeography can be approached only by the taking of mass collections throughout a large area. In many regions phases of these problems can be studied by local botanists. Here, perhaps, is the justification for this publication of results based on fragmentary evidence.

In the Arrowhead Country of Minnesota, and in adjacent Ontario, mass collections should affirm or disprove the suggestion that var. *hypomalaca* is indifferent to temperature. Is it really absent from the north shore of Lake Superior? Would collections from north of the lake show the range of the variety to be continuous from Duluth to Sault Ste. Marie and eastward? There are but 2 mass collections, comprising 8 individuals, between Sault Ste. Marie and Door County, Wisconsin; is the variety actually isolated in Door County? Would a series of mass collections from the tip of Bruce Peninsula southward show a cline? And what of the species as it occurs north of the regions represented by these mass collections? A botanist driving north from North Bay would have opportunity to determine whether the variety becomes less abundant again northward, or if it finally replaces entirely the glabrous plant.

SUMMARY

Diervilla Lonicera shows 3 types of pubescence, each of which has a different manner of occurrence. (1) Plants with densely pilose lower leaf-surfaces occur in 3 regions, one north of Lake Huron, another west of Lake Michigan, and a third in northern Minnesota. They are nearly always accompanied by other individuals with glabrous leaves, and show clines to the south, east and west from a center of high percentage just north of Lake Huron. Intermediates are rare. All these facts seem to justify the treatment of the pilose-leaved phase of *D. Lonicera* as var. *hypomalaca* Fernald. The clines show no relation to exposure, rock types, or local differences in temperature, apparently representing a purely geographic concentration. Var. *hypomalaca* may be a "submerged species," or may be the result of the infiltration of the species by a pilose mutation. (2) The occurrence of leaves with midrib and/or veins setulose below is sporadic throughout the range of the species, and such leaves may even occur on the same plant with perfectly glabrous leaves. (3) Ciliation of leaves and calyx-lobes is essentially uniform throughout the species.

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INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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(See also under Genetics: **Hubricht & Anderson**)

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